Dwarfmistletoe of Ponderosa Pine in the Southwest

by

FRANK G. HAWKSWORTH

Rocky Mountain Forest and Range Experiment Station
Forest Service

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By **Frank G. Hawksworth**

Plant Pathologist, Rocky Mountain Forest and Range Experiment Station,[1] Forest Service

INTRODUCTION

The damage caused by dwarfmistletoes (*Arceuthobium* spp.) has been rated as second only to that induced by heart rots in western coniferous forests (Gill 1935, p. 117). Because severe losses to heart rots are typically associated with mature and overmature stands, the magnitude of such losses should decrease as the harvesting of old stands continues. However, dwarfmistletoes will be of considerable importance in second growth also, since they attack trees of all ages. In the future, therefore, when most of the virgin stands will have been cut, it is expected that control of dwarfmistletoes will be the most pressing problem in forest pathology in the West. In some regions, notably in the Southwest (Arizona and New Mexico), these parasites are already the most serious pathogens.

The investigations reported here are on *Arceuthobium vaginatum* (Willd.) Presl f. *cryptopodum* (Engelm.) Gill, which is the most important pathogen of ponderosa pine (*Pinus ponderosa* Laws.) in the Southwest. These studies are designed to provide a more complete understanding of the parasite and its relationships with ponderosa pine. Ultimately, this information should help serve as a foundation for the development and refinement of silvicultural control measures.

This bulletin consists of seven major sections, the first of which is a general review of southwestern ponderosa pine dwarfmistletoe based on published information and on data from the present investigations. The other six sections deal with specific studies on the parasite: (1) life history as determined by inoculations, (2) seed flight, (3) seed dispersal period, (4) rate of spread, (5) effects on growth rate of the host, and (6) witches'-broom formation.

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[1] The author is on the staff of the Fort Collins Forest Disease Laboratory, Rocky Mountain Forest and Range Experiment Station, which maintains central headquarters at Fort Collins, Colo., in cooperation with Colorado State University. This work was conducted at the Forest Disease Laboratory, Albuquerque, N. Mex.

This publication is based on a dissertation submitted to the Graduate School of Yale University in partial fulfillment of the requirements for the Ph. D. degree.

REVIEW OF INFORMATION ON PONDEROSA PINE DWARFMISTLETOE

This review of *Arceuthobium vaginatum* f. *cryptopodum* and its pathological relationships with its host, *Pinus ponderosa*, is based on published information, and on investigations and observations made in the Southwest from 1950 to 1958. Although this species has been the most intensively studied western dwarfmistletoe, much remains to be learned about it. The first detailed, nontaxonomic account is that by MacDougal (1899), who discussed seed dissemination and distribution of the species at Grand Canyon, Ariz. Korstian and Long (1922) report an intensive study on the effects of the parasite on growth rate, mortality, and seed production in ponderosa pine, and offer suggestions for control. Pearson's (1950) monograph on the management of ponderosa pine in the Southwest includes a section on dwarfmistletoe, with information on mortality in infected stands and on the effects of the parasite on the growth rate of its host. Gill (1954) discusses the life history of the species and gives recommendations for its control. Recently, a Forest Pest Leaflet on this parasite has been issued (Andrews 1957). *Arceuthobium* in the United States was monographed by Gill (1935), and the genus as a whole has been reviewed by Kuijt (1955).

NOMENCLATURE

Arceuthobium vaginatum was first described from an undetermined five-needled pine in the State of Vera Cruz, Mexico. Early collection of the species from *Pinus ponderosa* in the northern parts of its range was described under the names *A. cryptopodum* Engelm. (*Razoumofskya cryptopoda* Coville) and *A. robustum* Engelm. (*R. robusta* Kuntze). These were reduced to synonomy under *A. vaginatum* by Gill (1935, p. 178), but the northern host-form on *P. ponderosa* was maintained and designated *A. vaginatum* f. *cryptopodum* (Engelm.) Gill. Gill (1935, p. 175) did not designate the predominantly Mexican form of *A. vaginatum* as a forma *typicum*, because of the scanty material available for study. The name *A. vaginatum* f. *vaginatum* is used here. This is in accordance with recent changes in botanical nomenclature wherein a species is considered as the sum of its varieties. Whenever a variety is named, another (the typical variety) is automatically created to contain the type, and it bears the specific epithet repeated without author citation (Lanjouw 1952).

No completely satisfactory or generally accepted common names for the various species of *Arceuthobium* have been proposed. A number of common names for *A. vaginatum* f. *cryptopodum* have been used, but most of these attempt to distinguish this species from *A. campylopodum* f. *campylopodum* on ponderosa pine on the Pacific coast, and such names become too cumbersome to be useful.[2] In this paper, unless stated otherwise, the use of the terms "dwarfmistletoe" or "mistletoe" will refer to *A. vaginatum* f. *cryptopodum*.

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[2] Common names suggested for this species include Rocky Mountain yellow pine dwarf-mistletoe (Hubert 1951), Intermountain yellow pine mistletoe (Weir 1923), western yellow pine mistletoe (Korstian and Long 1922), Southwestern ponderosa pine dwarfmistletoe (Hawksworth 1956), and hidden footed small mistletoe (Daniels 1911).

HOSTS

Arceuthobium vaginatum (forms *vaginatum* and *cryptopodum*) has been recorded on 11 pines and on 1 species of true fir. *A. vaginatum* f. *cryptopodum* is of economic importance only on *Pinus ponderosa* Laws., although it has been found in Colorado on *P. contorta* Dougl. ex Loud. and *P. flexilis* James (Hawksworth 1956, Hawksworth and Peterson 1959).

The known hosts of *Arceuthobium vaginatum* f. *vaginatum* are recorded below:

Host	*State and country*	*Reference*
Abies religiosa Schlecht. & Cham	Mexico, Mexico	Gill 1935
Pinus hartwegii Lindl	D.F., Mexico	Roldan 1924
P. montezumae Lamb	Tlaxcala, Mexico	Sosa 1939
P. tenuifolia Benth	———, Mexico	Kuijt 1955
P. pseudostrobus Lindl	Michoacan, Mexico.	Hawksworth 1961
P. leiophylla Schlecht. & Cham	Tlaxcala, Mexico	Sosa 1939
P. l. var. *chihuahuana* Shaw	Arizona, U.S.A	Gill 1935
P. arizonica Engelm	Coahuila, Mexico	Johnston 1944
Do	Arizona and New Mexico, U.S.A.	Gill 1935
P. engelmannii Carr	Arizona, U.S.A	Gill 1935

The parasite undoubtedly occurs on other Mexican pines. The report by Rydberg (1922) of *Pinus jeffreyi* Murr. as a host for *Arceuthobium vaginatum* is considered erroneous, since so far as is known it is not found within the range of this tree. Also, Standley and Steyermark's (1946) report of the species on *Cupressus* in Guatemala should be verified.

GEOGRAPHIC RANGE

The geographic range of *Arceuthobium vaginatum* extends over 25 degrees of latitude, from Guatemala to northern Colorado. The exact ranges of f. *vaginatum* and f. *cryptopodum* are not known, but the United States collections (except for the Mexican border region of Arizona and New Mexico) have been referred to the latter form (Gill 1935, p. 178). A general range map showing the known distribution of *A. vaginatum* is given in figure 1, and that of f. *cryptopodum* in the United States in figure 2. The parasite occurs throughout the ponderosa pine forests of Arizona, New Mexico, and Texas. It is less widespread in Nevada, Utah, and Colorado. It is known in one county in Nevada and seven counties in southern Utah. It is generally distributed in southern Colorado and extends north along the eastern slope of the Front Range nearly to Wyoming. The distribution maps (figs. 1 and 2) are based on published information and on observations and collections made by the writer and others (see appendix).

IMPORTANCE OF DWARFMISTLETOE IN THE SOUTHWEST

It has been generally recognized for some time that dwarfmistletoe is the most important disease agent of ponderosa pine in the Southwest. However, information on the abundance of the parasite and on the amount of damage it causes has only recently become available

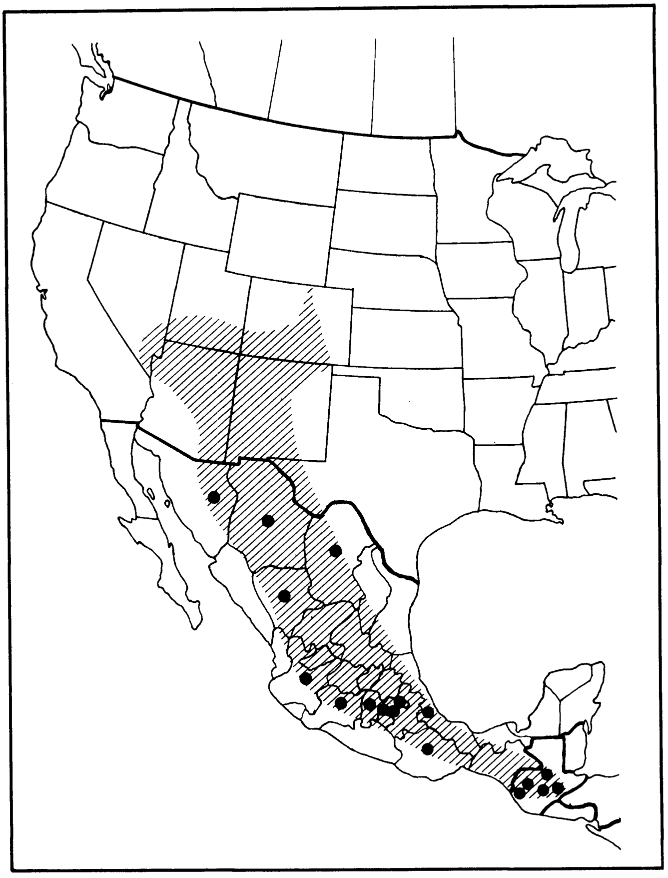

FIGURE 1.—The known distribution of *Arceuthobium vaginatum* (forms *vaginatum* and *cryptopodum*) in Guatemala, Mexico, and the United States. The dots indicate Mexican States and Guatemalan localities where the parasite has been reported.

(Andrews and Daniels 1960). This survey of the commercial forests of Arizona and New Mexico indicates that 36 percent of the ponderosa pine stands are infected. The parasite is present on an estimated 2½ million acres in the two States.

Volume loss through growth reduction of trees infected by dwarfmistletoe is thought to be at least as great and probably greater than losses due to mortality. Andrews and Daniels (1960) estimate that combined volume losses in ponderosa pine in Arizona and New Mexico approximate 150 million board feet annually. Andrews (1957) states that this dwarfmistletoe is responsible for a 16 percent reduction in sawtimber growth in the Southwest.

Studies made on the Fort Valley Experimental Forest, Ariz., (Pearson and Wadsworth 1941) indicate that three agencies—dwarfmistletoe, wind, and lightning—accounted for more than 90 percent of the mortality in cutover stands during a 30-year period. In the 480-acre area on which this information was based, mortality due to dwarfmistletoe was responsible for 38 percent of the loss in volume

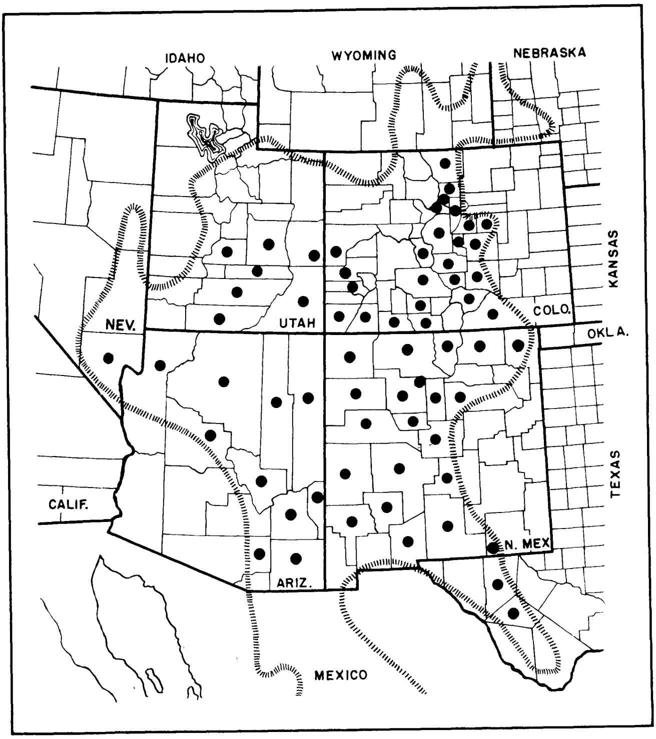

FIGURE 2.—The known distribution of *Arceuthobium vaginatum* f. *cryptopodum* on ponderosa pine by counties in the United States. The approximate limits of ponderosa pine in this area are indicated by the broken line.

and 51 percent of the trees killed. Pearson (1950, p. 74) points out that mistletoe-associated mortality is highly variable because of the irregular distribution of the parasite.

A recent survey of the Mescalero-Apache Reservation in southern New Mexico (Hawksworth and Lusher 1956) indicates that dwarfmistletoe is the primary disease problem of ponderosa pine in this area also. The parasite was present in 53 percent of the ponderosa pine acreage, and 37 percent of the merchantable ponderosa pine gross volume was in infected trees. Mortality was nearly twice as high in infected as in uninfected stands.

Although ponderosa pine dwarfmistletoe is generally distributed throughout the Southwest, its abundance in different parts of the area is quite variable. In general, it is most abundant in the White and Sacramento Mountains in southern New Mexico and along the Mogollon Rim in central Arizona.

DESCRIPTION OF THE PLANT AND ITS LIFE HISTORY

Shoots

The shoots, or that part of the dwarfmistletoe plant which is outside the tissues of the host, are described in detail by Gill (1935, p. 121). These shoots arise from the endophytic (or root) system of the parasite and not directly from the embryo. They are segmented (figs. 3 and 4) and leafless, the leaves being reduced to a single pair of minute scales at the top of each segment. The shoots are usually square at the base, but they may be somewhat circular in cross section at the top.

The anatomy of *Arceuthobium* shoots differs markedly from typical dicotyledonous stems (Gill 1935, p. 123). There is no central xylem cylinder, but a number of distinct xylem strands occur near the center of a parenchymatous matrix. Apparently, there are no phloem tissues in the shoots. The young stems have a single layer of epidermis, but this is gradually replaced in older shoots by a secondary cuticularized layer. The vascular system of *A. vaginatum* f. *vaginatum* shoots is described by Tubeuf (1919, p. 262).

In mature plants, the shoots average 10 to 15 centimeters high and 3 to 5 millimeters in diameter. The largest shoots seen for this species were 27 centimeters high and about 1 centimeter in diameter at the base. Female shoots are usually somewhat larger than male shoots of the same age.

The shoots of this species are usually some shade of red or orange. However, shoots of many other colors such as purple, green, yellow, or even black may be found. The characteristic orange or red color makes it relatively easy to detect the parasite among the green foliage of its host. Shoots growing in shaded parts of the crown tend to be greener than those in more exposed areas. Gill (1935, p. 122) suggests that shoot color is determined to a large degree by external factors such as light, temperature, and latitude. However, certain heritable influences also seem to be involved, as infections with markedly different colored shoots may occur next to each other on the same branch.

The shoots are perennial and bear several successive crops of flowers. MacDougal (1899) and Korstian and Long (1922, p. 4) are wrong in stating that shoots die after the fruits mature. The maximum age attained by shoots is not known, but it appears to be at least 5 to 10 years.

Once established, the endophytic system of the parasite extends distally and proximally along the stem, and new shoots are continually produced at points farther from the original point of infection. As the older shoots die, they are replaced by new ones from the same endophytic system. The production of new shoots proceeds along a branch at a rate of ½ to 1 centimeter a year in each direction. Infections on the main stem of seedlings and saplings spread up and down the trunk at a rate of 1 to 2 centimeters a year in each direction. The rate is dependent on host vigor; it is nearly twice as fast in dominant as in suppressed trees.

Two types of shoot distribution have been reported for various species of *Arceuthobium* (Gill 1935, p. 123): the shoots may occur in tufts or they may be scattered along the twigs. Both types are common in *A. vaginatum* f. *cryptopodum*. Gill supposed that this difference in habit is more a function of the host than anything inherent in the mistletoes, and the results of the present study confirm this. Infections where shoots are scattered along the branch (systemic infections) are apparently the result of stimulation of dormant whorl buds or possibly needle fascicle buds. If buds are not stimulated, the infection remains

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FIGURE 3.—Shoots of *Arceuthobium vaginatum* f. *cryptopodum*. *A*, A female plant, showing the fruits about 3 months before maturity (× 0.5). *B*, a male plant showing the flowers at the time of pollination (× 0.4). Both collections made in May on the Fort Valley Experimental Forest, Ariz.

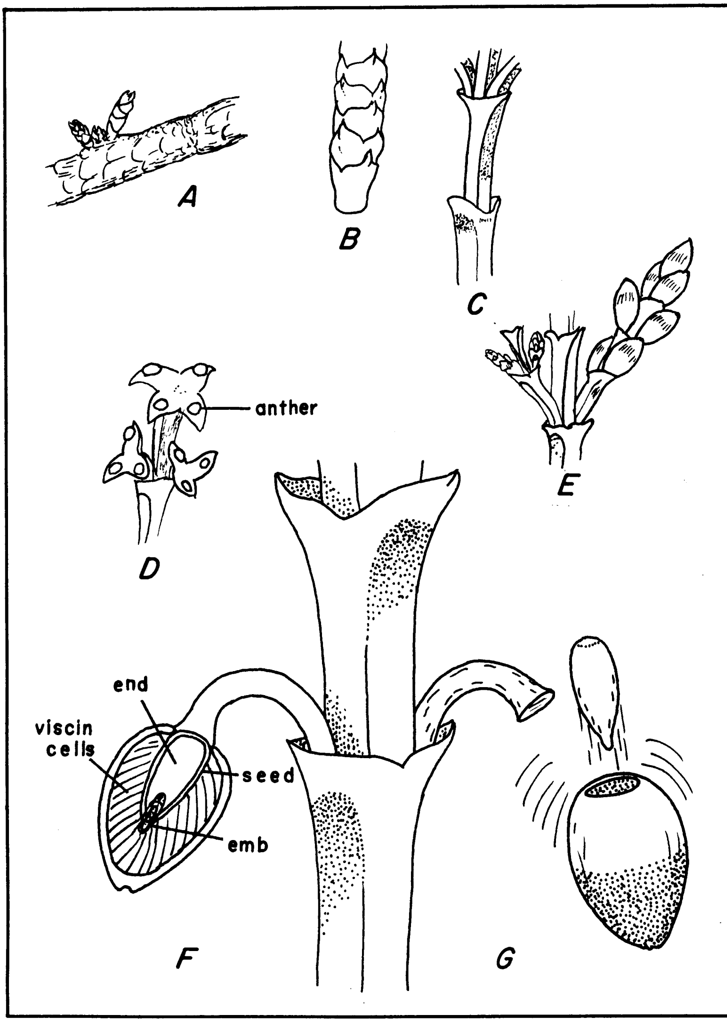

FIGURE 4.—Dwarfmistletoe shoots, flowers, and fruits. *A*, A young infection showing shoots just emerging from the bark of a host twig (× 1). *B*, Part of a young shoot showing the decussate arrangement of the segments (× 1). *C*, An older shoot in which the segments are elongated and square in cross section (× 1). *D*, Part of a male plant, showing the conditions of the flowers just before the anthers open; two lateral 3-partite flowers and a terminal 4-partite flower (× 2). *E*, Part of a female plant showing the condition in late spring. The shoot on the left has many flowers that have just been pollinated; the shoot on the right has several immature fruits about 2 months from maturity (× 1.5). *F* and *G*, Longitudinal sections of the mature fruit, showing the seed and dispersal mechanism (× 4.5). *F*, A mature fruit before the seed is expelled, showing how the pedicel of the fruit is elongated and recurved so that the original apex of the fruit is now pointed downward. The gross anatomy of the fruit showing the seed, embryo, endosperm, and viscin cells. *G*, A mature fruit immediately after the discharge of the seed. The fruit is severed from the pedicel and the seed is ejected from the fruit and propelled upwards.

as the tufted type. The stimulation of ponderosa pine buds by dwarfmistletoe is discussed further on page 98.

For main stem infections, there is an inverse relationship between age and shoot production. That is, shoots are rarely formed on the old part of the bole, and those that do appear are relatively feeble and produce few mature fruits.

Flowers

All species of *Arceuthobium* are dioecious. Because of multiple infections, male and female plants usually occur intermingled in the same tree. The results from inoculations plus a count of 1,000 natural infections indicate that a 1:1 sex ratio exists for this species.

Staminate Flowers

The gross structure of the staminate flowers is simple (Gill 1935, p. 127). Each flower consists of a whorled, usually 3-partite perianth. Each segment contains a single sessile, cushion-shaped anther (fig. 4, *D*). Counts of 5,000 flowers in two localities in northern Arizona showed that 94 percent were 3-partite; 5 percent, 4-partite; and 1 percent, 2-partite. Terminal flowers are more frequently 4-partite than lateral ones. The bright-yellow pollen is produced from April to June, although most plants flower in May or June. The open flowers have a distinctive, but difficult to describe, odor that apparently has not been previously recorded. Male flowers are shed after the flowering period.

Pistillate Flowers

The small elliptic pistillate flower consists of two lobes that are almost entirely fused with the perianth and with the central pistil (Gill 1935, p. 132). The style projects slightly above the perianth. With the exception of the dark stigma, all structures are about the same color as the shoots. Aberrant three-partite pistillate flowers have been found in *Arceuthobium vaginatum* f. *vaginatum* (Gill 1935, p. 174).

Stigmatic secretions have been observed in *Arceuthobium americanum* (Dowding 1931) and in *A. oxycedri* (Heinricher 1915). They have also been found in *A. vaginatum* f. *cryptopodum* where they are particularly conspicuous early in the morning during the flowering period (May to June). The clear, sweet-tasting droplets average about 1 millimeter in diameter.

Pollination

The structure of flowers and pollen of *Arceuthobium* suggests that these plants are entomophilous, but the insects involved have not been determined for most species. Weir (1915, p. 375) observed unnamed hymenopterous insects taking part in the pollination of drawfmistletoes in the Northwest, and Kuijt (1955, p. 585) observed ants visiting male plants of *A. americanum*.

Observations made in the Southwest suggest that thrips are the primary pollinating insects of *Arceuthobium vaginatum* f. *cryptopodum*, although no experiments have been conducted to determine this conclusively. Thrips were found on this mistletoe in Arizona, New Mexico, Colorado, and Utah. In fact, they were found on nearly every plant examined. During the pollen season, these normally dark insects appear to be yellow because of the pollen on their bodies. Collections of thrips were submitted to Miss Kellie O'Neill of the Insect Identification and Parasite Introduction Section of the U.S. Department of Agriculture. The most abundant thrips were an undescribed species of *Frankliniella*, but *F. occidentalis* (Perg.) and *Thrips tabici* Lind. were also present.

Fruits

The fruits of *Arceuthobium vaginatum* f. *cryptopodum* are ovoid and measure about 3 by 5 millimeters at maturity. The color is similar to that of the shoots, although the upper and lower parts of the fruit are of different shades. The fruiting period of this species lasts for about 3 weeks, usually the last week in July and the first 2 weeks in August, and it was intensively studied in 3 successive years at one locality in northern Arizona (page 62). Fruits of other North American species of *Arceuthobium* mature in the autumn.

Each fruit contains a single seed which, at maturity, may be forcibly expelled for a considerable distance. The anatomy of the fruit and the expulsion mechanism are discussed by Gill (1935, p. 137). In brief, the process is as follows. As the fruits approach maturity, the pedicel is elongated and reflexed so that the stigmal end points downward. An abscission layer is formed between the tip of the pedicel and the base of the fruit. The oblong viscin cells (fig. 4, *F*) surrounding the seed imbibe water and eventually build up a great pressure within the fruit. Finally, the abscission layer gives way and the fruit is separated from the pedicel; at the same instant, the fruit coat contracts rapidly and the seed is forcibly ejected and propelled upwards (fig. 4, *G*).

In the plants that developed from inoculations, fruits were first produced in the sixth, seventh, and eighth years after infection. About 60 percent produced their first fruits in the seventh year.

Seeds

Members of the mistletoe family have such unusual "seeds" that the term must be used with reservation. In contrast to true seeds, those of *Arceuthobium* have no seed coats or integuments but are only a naked embryo and endosperm encased in the endocarp of the fruit (Gill 1935, p. 137).

The freshly expelled seeds are olive green except for the basal end, which is yellow, but after a few days they turn reddish brown and the basal end turns orange. They are coated (except for the basal end) with a mucilagenous substance called viscin. This material enables the seed to stick to the surface on which it alights (fig. 5, *A*). Also, since the viscin is hygroscopic, it is thought to play a part in supplying water necessary for germination (Gill 1935, p. 139). During wet periods, the viscin coat of the seed imbibes water and the seed becomes

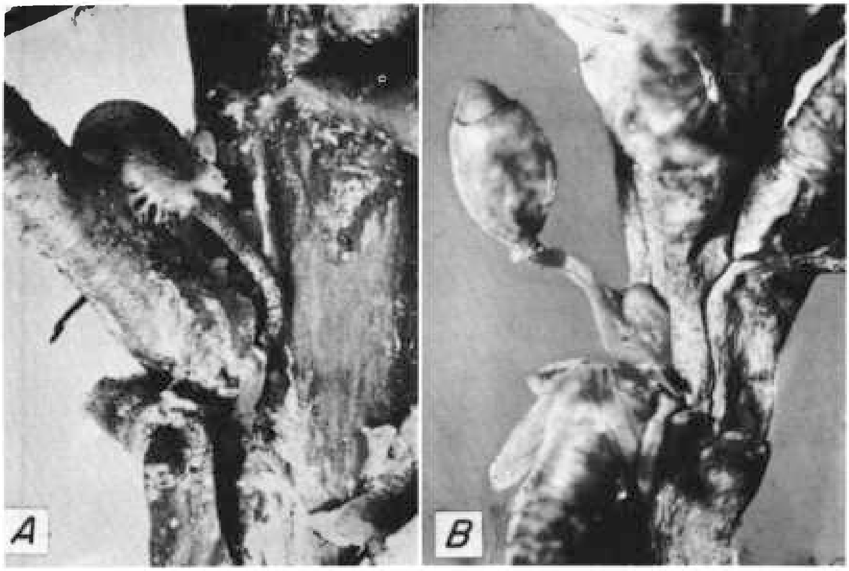

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FIGURE 5.—Germinating dwarfmistletoe seeds. *A*, A seed in place 2 months and germinating at the base of a needle fascicle on a 3-year-old ponderosa pine twig. The tip of the hypocotyl is beneath the needle fascicle. Note the viscin strands holding the seed to the needle. *B*, A seed in place 1 year, showing the development of the holdfast at the tip of the hypocotyl, which has been exposed by bending back the needle fascicle. Both approximately × 8. From Gill (1954).

surrounded by a jellylike mass. The viscin eventually loses its hygroscopic quality and acts only as a cement.

The gross internal structure of the seed is shown in figure 4, *F*. The small embryo is at the distal end, and the cotyledonous tips are scarcely distinguishable. Both the endosperm and the embryo have a high chlorophyll content.

The seeds are oblong, hemispherical at the basal end (which is the forward end when the seed is ejected from the fruit), and pointed at the other. Common variations in size and shape of the seeds are shown in figure 6, *A*. The seeds are typically 2½ to 3 millimeters long and about 1 millimeter in diameter. Average dimensions of 200 seeds from one locality in northern Arizona were 2.9 by 1.1 millimeters. Seeds from central New Mexico and northern Colorado were slightly smaller and averaged 2.4 by 1.0 millimeters (100 seeds) and 2.7 by 1.1 millimeters (30 seeds), respectively.

Polyembryonic and Abnormal Seeds

Weir (1914) noted that 3 seeds in a lot of 20 of *Arceuthobium vaginatum* f. *cryptopodum* developed 2 radicles instead of 1. He stated that such diembryonic seeds were morphologically indistinguishable from normal ones. On the basis of Weir's results, it might be assumed that such polyembryony is relatively common in this species, but the writer has not observed a single instance of this type.

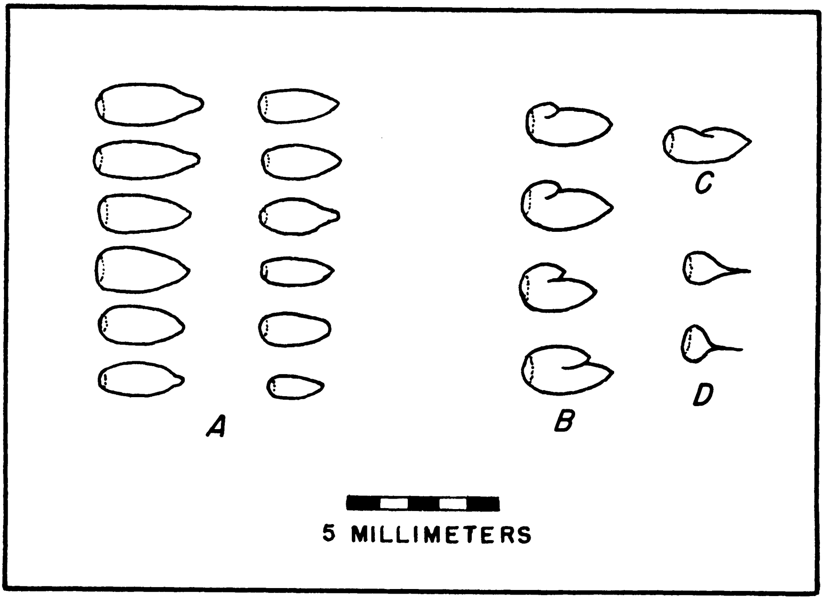

FIGURE 6.—Normal and abnormal dwarfmistletoe seeds. *A*, Variation in size and shape of normal seeds. *B*, Fused seeds that consist of two unequal elements. *C*, A rare abnormal form with an indented side. *D*, Rare aborted seeds in which only the basal part is fully developed.

However, a morphologically distinct type of diembryonic seed is occasionally found in nearly all collections of this species. It consists of a normal-sized seed to which a secondary seed is fused (fig. 6, *B*). Each element consists of a separate endosperm and embryo enclosed in a common endocarp. Although such seeds have two apparently normal embryos, it has not been determined whether both will produce hypocotyls. Counts of 5,000 seeds showed that this abnormality occurred in about 1 percent, with the frequency in individual lots ranging from 0.4 to 3.3 percent. Two other types of abnormal seeds (fig. 6, *C* and *D*) were found, but these are even rarer than the fused seeds.

Seed Dispersal

MacDougal (1899) stated that the seeds of this species were expelled to distances of 2 to 3 meters. In the studies reported here, the maximum horizontal distance of seed flight (to a point at the same level of the point of discharge) was 42.0 feet with an average of 17.4 feet (page 52).

Distances of infection measured from the bole of the source tree are greater than the actual distance of the seed flight, since in most cases the seed origin is some distance out from the bole. Distances of infection from mature trees were reported by Gill and Hawksworth (1954) for nearly 2,000 seedlings; 99 percent of these were within 55 feet. Although winds are considered important aids in the seed dispersal for some species of *Arceuthobium* (Weir 1916, p. 34; Roth 1953), this does not seem to apply for *A. vaginatum* f. *cryptopodum* (Gill and Hawksworth 1954).

Part of the present investigation dealt with the ballistics of dwarfmistletoe seed flight, and results suggest that height of the infection has little effect on horizontal distance of seed flight. Average angle of discharge of seeds was approximately 30° to 40° from the horizontal. The average initial velocity of the seeds is estimated to be about 45 feet per second (Hawksworth 1959a).

Dwarfmistletoe seeds are scattered about in all directions. Many fall to the ground, and others land on nonsusceptible parts of the pines, such as old bark or needles. Only a small proportion of them manages to germinate on young twigs, which is essential to induce infection. Some land directly on twigs; others alight on needles and are washed by rain onto the twigs. Roth (1959) found that for *Arceuthobium campylopodum* f. *campylopodum* on ponderosa pine in Oregon, practically all the seeds on the twigs were first intercepted by needles and then washed by rain onto the branches. Although no quantitative information is available for *A. vaginatum* f. *cryptopodum*, observations suggest that pine needles are also important in intercepting seeds of this species.

Little is known of the vectors in long distance spread of dwarfmistletoe, but it is presumed that birds are involved.

Germination

Seeds of *Arceuthobium vaginatum* f. *cryptopodum* germinate within about 1 month after they are expelled. Germination occurs during the summer rainy season that is characteristic of most areas where the species is found. Summer germination is unique in this species; the other dwarfmistletoes germinate in the spring after overwintering on the host.

Before the hypocotyl emerges, the seeds darken and swell to about 1½ times their original diameter. The slender, reddish hypocotyl is about 0.5 millimeter in diameter (fig. 5, *A*). If the hypocotyl does not come in contact with the host, it may attain a length of about 15 millimeters before the endosperm is exhausted of its food supply.

Little is known of the tropisms of the hypocotyls of the North American species of *Arceuthobium*, although the European species *A. oxycedri* is both negatively phototropic and negatively geotropic (Heinricher 1917). Observation of the hypocotyls of *A. vaginatum* f. *cryptopodum* indicates that this species is at least negatively phototropic, but laboratory tests are needed to determine the intensity of this response and to compare it with a possible geotropic response.

On the basis of limited samples, germination rates of 40 to 50 percent were noted for naturally dispersed seeds left in place. The seeds can germinate without a living host.

Establishment

Only a very small proportion of the dwarfmistletoe seeds is deposited on susceptible host tissue. Results of inoculations indicate that of those deposited on such tissue, only about 5 percent become established. Insects and other agents destroy a great many seeds and, as previously mentioned, only about half of the seeds germinate.

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The hypocotyl grows along the surface of the host bark either until its food supply is exhausted or until a depression or obstacle such as a needle fascicle, needle scar, sterile scale, or bud is encountered. When the tip of the hypocotyl touches one of these objects, a mound of tissue develops at the tip (fig. 5, *B*). The hypocotyl functions as a holdfast from which a primary absorbing "root" or haustorium develops and penetrates the cortex of its host; this is the beginning of the endophytic system of the parasite.

Another possible mode of entrance of this species is through the interior of the needle fascicle. Germinating seeds are occasionally found with the radicle extending to the base of the fascicle, but it has not been determined whether infection can be accomplished in this manner. In inoculation tests with this parasite, no infection took place through wounds, presumably because of the extensive resin flow.

Endophytic System

The endophytic system of dwarfmistletoe (Gill 1935, p. 139) is made up of two parts: (1) the cortical system that develops in the cortex of the host, and (2) the sinkers that occur in the xylem tissue of the host.

The cortical system includes the primary haustorium and its branches, which range throughout the cortex in an irregular manner. The haustoria grow faster longitudinally than laterally along the branch. The cortical system maintains its position in the active phloem tissues of the host by centripetal growth. When strands of the cortical system come in contact with the cambial region of the host in the vicinity of a ray, a sinker is formed (Gill 1935, p. 140).

The sinkers are wedge shaped in a cross section of the host stem and are radially alined. They occupy the rays, appearing as enlarged rays, and are readily detectable macroscopically (fig. 7). Sinkers do not penetrate xylem already formed, but they become imbedded as new xylem is laid down around them. The sinkers maintain contact with the cortical system of the parasite by a meristimatic area in the vicinity of the host cambium. This enables them to grow at a rate corresponding to the radial growth of the host stem.

Shoots are usually not formed for some time after the plant is established. In inoculations with this dwarfmistletoe, more than 90 percent of the infections first produced shoots during the third, fourth, and fifth years after the date of planting, although in one case 8 years elapsed between infection and initial shoot production.

PHYSIOLOGY

Little is known of the physiology of dwarfmistletoes (Kuijt 1955). The most obvious physiological requirement of a dwarfmistletoe plant is, of course, a susceptible host, but nothing is known of the factors that determine the susceptibility of a host species.

Some writers suspect that dwarfmistletoes manufacture no carbohydrates, while others claim that they absorb only water and minerals from their hosts (Kuijt 1955). Actually, these parasites are probably intermediate between those two extremes. Since the shoots contain

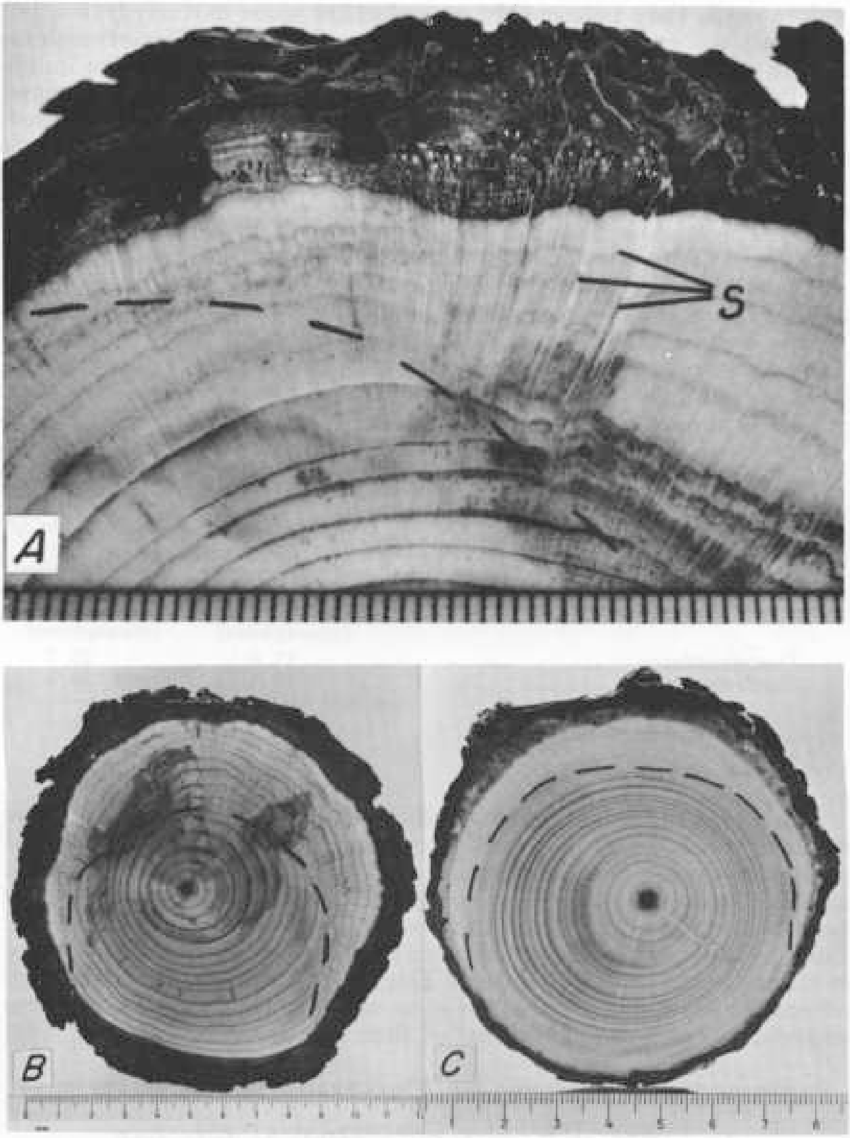

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FIGURE 7.—Cross sections of ponderosa pine stems, showing dwarfmistletoe sinkers and hypertrophy of the host tissues. *A*, The wood above the dashed line is invaded by the parasite, and numerous sinkers (s) are visible (× 2). *B*, Smaller scale view of the same stem. The infected part of the stem is indicated by the dashed line. Note the indented growth rings and the resin infiltration in the infected parts of the stem. Infection established for 11 years on 17-year-old stem (× 0.5). *C*, Cross section of a slower growing stem, showing the thickened bark in the infected tissues. Nearly three-quarters of the circumference of the stem is infected (dashed line). Infection established for 16 years on 33-year-old stem (0.75). Millimeter scale shown in each photograph.

chlorophyll, they presumably manufacture some carbohydrates, but certainly not enough to meet all their requirements. Dwarfmistletoe plants are not dependent on shoots for survival; they can live indefinitely without producing shoots in old, thick barked ponderosa pines. Thus, *Arceuthobium vaginatum* f. *cryptopodum* is sometimes, at least, a total parasite. The common occurrence of starch in the endophytic system of *Arceuthobium* (Dufrenoy 1936, Weir 1918) suggests that the carbohydrate supply of these plants is adequate.

Dwarfmistletoes have not yet been grown *in vitro*, although progress has recently been made in culturing infected host tissue (Blakely 1959). Although Blakely was not able to infect Douglas-fir callus with *Arceuthobium douglasii* Engelm. seeds, he did induce the endophytic system of the parasite to invade callus in tissue cultures of infected stems.

In general, the osmotic concentration of the cell sap of parasitic plants is higher than that of their hosts (Harris et al. 1930). Measurements of *Arceuthobium vaginatum* f. *cryptopodum* and ponderosa pine indicate that this is true here also, although the differences are slight:

	Osmotic pressure	
	Flagstaff, Ariz.[1] (*atmospheres*)	*Bryce Canyon, Utah*[2] (*atmospheres*)
Dwarfmistletoe	17.6	23.7
Ponderosa pine	17.1	20.1
Difference	.5	3.6

[1] Korstian 1924.
[2] Harris 1934.

The slight differences between the osmotic concentration of tissue fluids of the host and the parasite suggest that this might be a critical factor governing the distribution of dwarfmistletoe. For example, an osmotic concentration of the host that is too high to support the parasite might explain the absence of dwarfmistletoe at the lower limits of the ponderosa pine type in the Southwest. This possibility is strengthened by the finding of Harris et al. (1930) that the range of osmotic concentrations in mistletoes of the genus *Phoradendron* was considerably narrower than that of their host plants.

Pathological Aspects of Dwarfmistletoe Infection

Age of Host Growth Susceptible to Infection

Early studies by Weir (1918, p. 8) indicated that dwarfmistletoes are not able to become established on growth more than 3 years old. Results of the present study show that *Arceuthobium vaginatum* f. *cryptopodum* can infect ponderosa pine growth at least 9 years old. The current year's growth is the most susceptible, and susceptibility decreases with age. It has also been shown recently that *A. americanum* can become established on *Pinus contorta* growth up to 58 years old (Hawksworth 1954). The basis for the resistance of older tissues was thought by Weir (1918, p. 4) to be due to cork formation and the absence of exposed chlorophyllaceous tissues.

Results of tests reported here suggest that factors affecting the seed may also determine the amount of infection that takes place on growth of various ages. Seeds placed on older tissues are more apt to be destroyed by insects or removed by rains than seeds placed on recent growth. When placed on the needle-bearing parts of a twig (or roughly the last 4 to 6 years of ponderosa pine growth), they are somewhat protected and hence have a greater chance of remaining long enough to germinate and produce a new infection. Because the needle retention of ponderosa pine varies in the Southwest, this may have a bearing on relative susceptibility in different areas.

Infection in Relation to Tree Size

Infection is not common in seedlings, even though all stem growth on the tree may be susceptible, because such trees present a very small target area. In general, within an infected stand, the frequency of the parasite increases with tree size (fig. 8). The proportion of trees infected increased rapidly in the smaller diameter classes (19 percent in the 1-inch class to 57 percent in the 5-inch class), and then increased gradually to 100 percent in trees larger than 35 inches in diameter.

Influence of Tree Vigor on Infection

In contrast to most pathogens of forest trees, dwarfmistletoes are obligate parasites; that is, they can survive only on living hosts, and as such are directly dependent on the vigor of their hosts. While most disease agents develop most rapidly on trees of lowered vigor, the opposite is usually true of obligate parasites.

Arceuthobium vaginatum f. *cryptopodum* has larger, more robust shoots and produces more seed on vigorous ponderosa pines than it does on poor-vigor hosts. The rate of extension of the endophytic system of the parasite is nearly twice as rapid in the main stem of dominant as in suppressed trees.

Prolonged dwarfmistletoe infection results in lowered vigor of the host. It should be kept in mind that lowered vigor is a result rather than a cause of infection.

The direct relationship between vigor of the host and vigor of the mistletoe is not commonly understood. Many foresters in the Southwest believe that vigorous trees may "throw off" or outgrow the parasite. However, the only instances seen in which the parasite had been killed were clearly attributable to the killing of infected branches, and, of course, the parasite with them. Shading is the commonest cause of the death of low branches. Other causes include fire, insects, and rodents. A possible explanation for the erroneous belief that ponderosa pine trees can "throw off" dwarfmistletoe infections is the common occurrence of brooms caused by agents other than *Arceuthobium*. Brooms induced by the fungus *Elytroderma deformans* (Weir) Darker are sometimes confused with those caused by dwarfmistletoe, but the cause of the most common nonmistletoe brooms is not known. Because no mistletoe shoots are found in such brooms, some observers think that the tree has "overcome" a dwarfmistletoe infection.

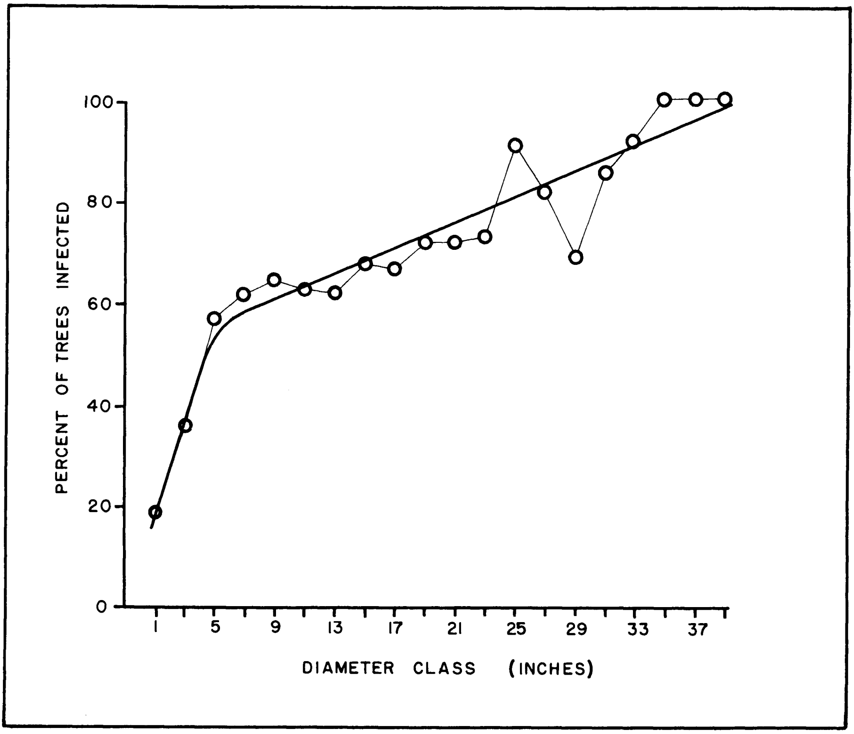

FIGURE 8.—Incidence of dwarfmistletoe in ponderosa pine in relation to diameter class, based on 16,710 trees on 83.4 acres of experimental plots in heavily infected stands in Arizona, Utah, and New Mexico.

How Dwarfmistletoe Weakens and Kills Its Host

The insidious effect of dwarfmistletoe is a result of the appropriation of water, minerals, and other nutrients by the parasite and infected parts of the lower crown at the expense of upper parts of the crown. Once a branch becomes infected, it is able to take more than its share of nutrients. Thus, the diameter growth of infected branches is greatly enhanced (Korstian and Long 1922, p. 17–19). Infected branches may become several times as large as uninfected branches in the same whorl, and they tend to persist long after the uninfected branches are shaded out. As progressively more and more nutrients are appropriated by infected branches, the vigor of the crown declines. Eventually, the effective photosynthetic surface area of the tree is reduced below that necessary to sustain it, and death results.

The length of time required for dwarfmistletoe to kill a tree is highly variable. Among the more important factors involved are age of the tree when infection occurs, amount of the parasite in the tree, vigor of the tree, and activity of secondary pests. A tree infected while young is more readily killed by the parasite than one infected later in life. Also, the amount of mistletoe in a tree affects its longevity, since there is little reduction in growth rate or vigor until more than two-thirds of its crown is infected. Trees of poor vigor are more readily killed by dwarfmistletoe than those growing vigorously. Secondary pests, particularly bark beetles, frequently determine the fate of heavily infected trees; as the vigor of such trees declines, their susceptibility to bark beetles increases. Bark beetle outbreaks often originate in heavily infected stands, and the killing may extend outward to nearby lightly infected or mistletoe-free trees. Phillips (1907) noted that ponderosa pines infected by dwarfmistletoe were more susceptible to late frost injury than were healthy trees.

Effects on the Host

Growth Rate

There have been a number of investigations on the effects of *Arceuthobium vaginatum* f. *cryptopodum* on the growth rate of ponderosa pine (Korstian and Long 1922, Sperry 1934, Pearson and Wadsworth 1941, Pearson 1950, and the present study, page 74).

Korstian and Long (1922) analyzed about 200 trees with various degrees of infection and concluded that there was little or no reduction in the growth rate of lightly infected trees but that there was a marked falling off of current growth of heavily infected trees. Radial increment during a 5-year period in heavily infected trees was only 12 to 14 percent of that of uninfected trees. The reduction in cubic-foot increment was somewhat less and ranged from 15 to 31 percent of that for the mistletoe-free trees. Sperry (1934) also noted a reduction in radial growth of heavily infected trees in Colorado, although his study was based on only 10 trees.

The growth rate of infected trees over a 30-year period on the Fort Valley Experimental Forest, Ariz., was reported by Pearson and Wadsworth (1941) and Pearson (1950, p. 164). There was no difference between uninfected and lightly infected trees, but the volume increment in heavily infected trees was 35 percent less than that of healthy trees. Pearson (1950, p. 85) also compared the growth rate over a 25-year period of stands that had various amounts of mistletoe (table 1). Gross growth in heavily infected stands was 140 board feet per acre per year as compared with 185 board feet in lightly infected stands. The differences in net growth were even greater, because of the higher mortality in the heavily infected stands.

In the present investigation, information was obtained on the growth rate of about 1,600 trees in one locality in southern New Mexico. Trees with various degrees of infection were sampled in two age classes and four dominance classes. The effect of dwarfmistletoe on recent radial increment was most pronounced where growth in heavily infected, dominant trees for a 5-year period was reduced by 35 percent in 55-year-old stands and 52 percent in 140-year-old stands. No significant reduction was apparent until at least two-thirds of the crown was infected. The effect of heavy infection on total volume, height, and diameter—the reduction of these averaged 36, 19, and 8 percent, respectively—was less pronounced than that on recent radial increment.

TABLE 1.—*Comparative annual growth rate and mortality per acre of ponderosa pine in dwarfmistletoe-infected stands over a 25-year period, 1909–34, Fort Valley Experimental Forest, Ariz.*

Amount of dwarfmistletoe [1]	Area	Gross volume per acre		Gross growth	Mortality	Net growth
		1909	1934			
	Acres	*Board feet*	*Board feet*	*Board feet*	*Board feet*	*Board feet*
Light	2.0	5,200	9,820	185	0	185
Moderate	9.6	5,470	9,540	169	6	163
Heavy	3.5	5,660	8,230	140	37	103

[1] Criteria for classifying stands or time of classification are not given.

Source: After Pearson 1950, p. 85.

Vigor

Heavy dwarfmistletoe infection lowers the vigor of the host. Korstian and Long (1922) showed that length of needles, length of needle-bearing stem, and volume of crown are all markedly reduced in heavily infected trees. They also noted that the leaves of heavily infected trees were lighter green than those of healthy ones. In the results reported here, the frequency of poor-vigor trees (those in which the upper third of the crown was thin or fading) was 10 to 30 times as high in heavily infected trees as in uninfected and lightly infected trees in the same stand.

Mortality

The mortality rate in heavily infected ponderosa pine stands is abnormally high (Korstian and Long 1922, Pearson and Wadsworth 1941, Pearson 1950, Gill 1954, Andrews and Daniels 1960, and Hawksworth and Lusher 1956).

Figures 9, 10, and 11 show three heavily infected ponderosa pine stands. Stands on the South Rim of the Grand Canyon are shown in figures 9 and 11. The basal area in living trees in a 10-acre plot in this stand decreased 11 percent between 1950 and 1955. Of the 32 merchantable trees on the plot that died during the 5-year period, 31 were heavily infected in 1950. An infection center in a virgin stand on the Fort Valley Experimental Forest is shown in figure 10. Here, the parasite has been responsible for the death of all merchantable trees in an area of about three-quarters of an acre.

Mortality in small plots on the Fort Valley Experimental Forest as reported by Pearson (1950, p. 85) averaged 0, 6, and 37 board feet per acre per year in lightly, moderately, and heavily infected stands, respectively (table 1).

In an intensive survey of a 200,000-acre area in southern New Mexico, annual mortality was estimated at 48 board feet per acre in infected stands and 27 board feet per acre in stands without dwarfmistletoe (Hawksworth and Lusher 1956). The difference was most pronounced in cutover stands where annual mortality rates were 40 and 12 board feet per acre for infected and healthy stands, respectively.

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FIGURE 9.—A general view of an infected ponderosa pine stand on the South Rim of the Grand Canyon, Ariz. Of the 11 merchantable-sized ponderosa pines visible, 5 (marked D) have been killed by dwarfmistletoe within about the past 5 years. The other six are infected (marked I or X), and two of these (marked X) show a marked decline in vigor and probably will be killed within 5 years.

Mortality in infected ponderosa pine pole stands was higher than in plots with no mistletoe (Hawksworth and Lusher 1956). This mortality count was based on dead, standing trees with bark intact. It is estimated that such trees represent mortality within the previous 4 to 6 years. A comparison of mortality in large poles (trees 7.6 to 11.5 inches d.b.h.) and small poles (trees 6 feet high and up to 7.5 inches d.b.h.) follows:

	Dead trees as proportion of total stand (living plus dead)	
	Large poles (percent)	*Small poles (percent)*
Mistletoe-free plots	3	9
Infected plots	7	12

Mortality on dwarfmistletoe-free plots was highest in dense pole stands, where natural suppression is a major cause of death. However, in mistletoe-infected areas, mortality was greatest in pole stands of low density.

Seed Production

Two studies have shown that the seed produced by dwarfmistletoe-infected ponderosa pine is affected adversely. Pearson (1912) found that the germination of ponderosa pine seeds was 78 percent from

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FIGURE 10.—A general view of an infection center in a virgin stand on the Fort Valley Experimental Forest, Ariz. Dwarfmistletoe has been responsible for the death of all merchantable-sized trees in an area of about three-quarters of an acre. In addition, most of the understory trees are infected. Productivity of the area will be low indefinitely or until the parasite is reduced.

healthy trees and 61 percent from infected ones. Korstian and Long (1922) conducted a more detailed study and found that there was a reduction in both quantity and quality of seed production by infected trees. They reported that the "reproductive value" (number of clean seeds per tree times number of clean seeds per pound times germination percent) was reduced by 62 percent in moderately infected trees and by 73 percent in heavily infected ones as compared with the healthy trees.

Morphological and Anatomical Effects

Hypertrophies

Swellings resulting from local stimulation of both xylem and phloem tissues are characteristic of most infections of *Arceuthobium vaginatum* f. *cryptopodum* on ponderosa pine. They are less conspicuous in

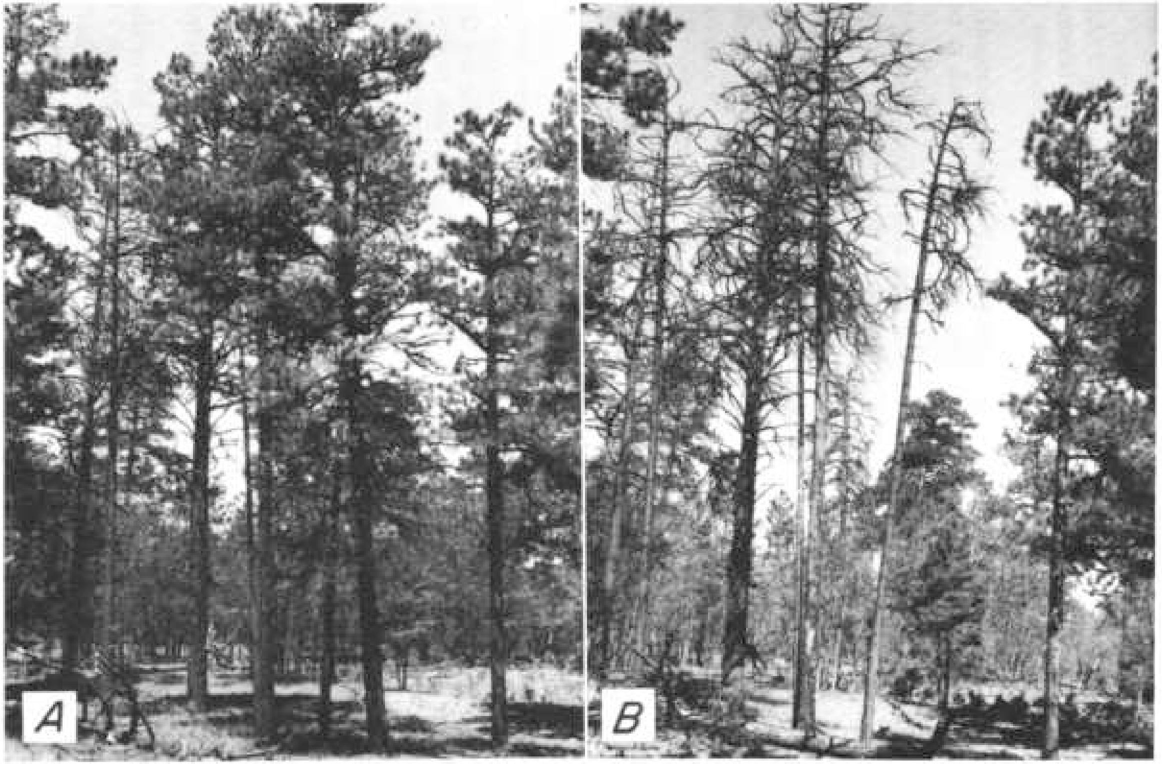

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FIGURE 11.—Effects of dwarfmistletoe in a heavily infected ponderosa pine stand on the South Rim of the Grand Canyon, Ariz. *A*, Taken in 1950. *B*, The same trees in 1955. Four trees averaging 12 inches d.b.h. were killed during the 5-year period.

main-stem infections than in branches. Since swellings usually precede shoot production, they provide a means for detecting incipient infections.

Witches'-Brooms

The most conspicuous symptom of dwarfmistletoe infection is witches'-brooms. These are growths of abnormal branching habit, often with unusually dense foliage. Three general types of brooms are found on ponderosa pine infected by *Arceuthobium vaginatum* f. *cryptopodum* (page 86).

The commonest type, which is here termed typical brooms, is usually much more abundant than the other two types together, and it accounted for 85 percent of the brooms in two stands in Arizona. These are approximately spherical in outline and may attain diameters of 12 feet or more. The branches are characterized by a marked taper (fig. 12).

The second type is termed volunteer leader brooms, because of a marked vertical tendency of the branches. The branches on the broom grow so fast that they may surpass the original main stem in both height and diameter. These accounted for about 15 percent of the brooms present in two stands examined. The proportion of brooms of this type is highest in young stands.

The third type is called weeping brooms, because the branches are geotropic. This type is relatively rare, and it accounted for less than 1 percent of the brooms in two stands studied. It differs from the other types in that the endophytic system of the parasite keeps pace with the terminal growth of the branches (systemic infection), and all growth on the branch is infected. In typical and volunteer leader brooms, the infection is localized at the center or base of the broom.

Why three different types are formed by the same parasite on the same host is not yet known. A series of young plants has been tagged, and observation of them should eventually provide an answer to this question.

Increased Branch Growth Rate

The diameter growth rate of dwarfmistletoe-infected branches is greater than that of healthy branches, and the rate is proportional to the amount of the parasite. For example, Korstian and Long (1922, p. 18) report that for a 5-year period the diameter growth of uninfected branches and those lightly, moderately, and heavily infected was 0.14, 0.16, 0.27, and 0.38 inch, respectively.

The large branches on infected trees (fig. 13 *A*, *B*, and *D*) lower the quality of the wood produced in such trees, but the actual amount of reduction has not been measured. These large limbs also make harvesting and slash disposal operations more costly. The lower boles of ponderosa pines are frequently scarred when the pitchy, broomed branches are burned (fig. 13, *C*).

Cankers

Occasional infections on the main stem of older trees are associated with necrosis of the bark and wood (fig. 13, *D*). Korstian and Long (1922, p. 19) describe "resin cankers" that are late stages of hyper-

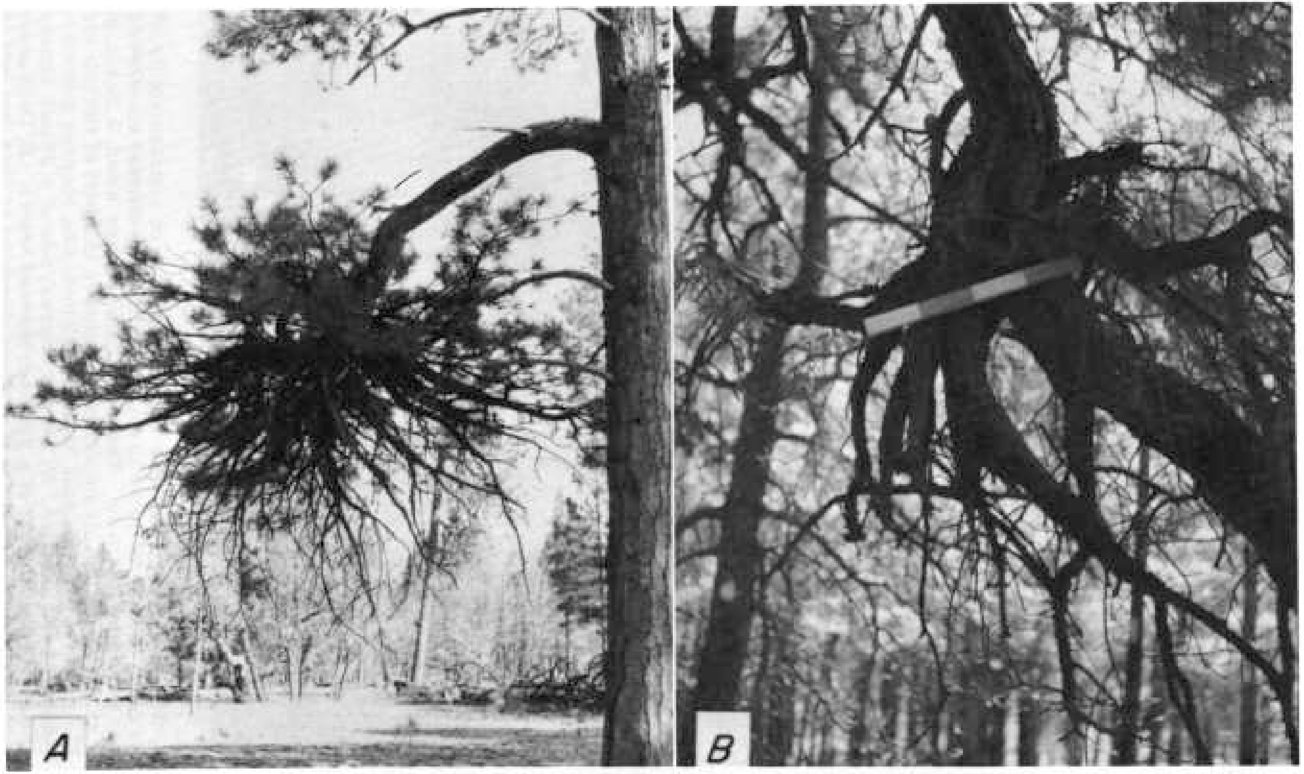

FIGURE 12.—Typical witches'-brooms in ponderosa pine infected by dwarfmistletoe. *A*, Large broom at the Grand Canyon National Park, Ariz. *B*, Closeup of the central part of an unusually large broom showing its size in comparison with a 2-foot rule. Fort Valley Experimental Forest, Ariz.

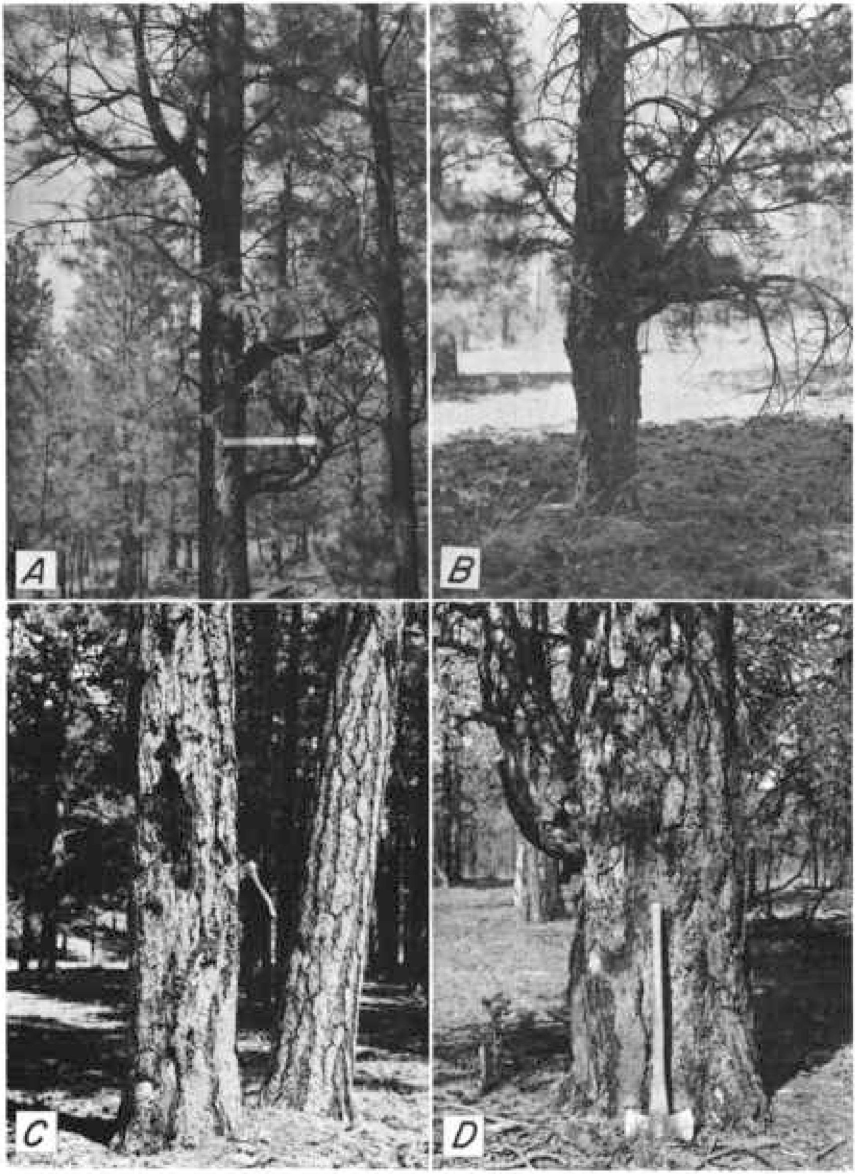

FIGURE 13.—Effects of dwarfmistletoe on the reduction of merchantability of ponderosa pine. *A*, Pole 12 inches in diameter with three infected branches on the lower 10 feet of the bole. These branches average about 5 inches in diameter at the bole, while all uninfected branches in this part of the bole are dead. *B*, An infection at the main stem of a 12-inch pole, showing distortion in the vicinity of the infection. *C*, Severely scarred bole of a 24-inch mature pine, caused by the burning off of a mistletoe-broomed branch. *D*, Dead areas on the bole of a mature ponderosa pine (note sloughing of bark just left of the top of the ax handle). Insect activity and sap rot as well as the large limb reduce the merchantability of this part of the bole. (*A*, Fort Valley Experimental Forest, Ariz. *B*, *C*, and *D*, Grand Canyon National Park, Ariz.)

trophies in which the sapwood is heavily infiltrated with resin and there is a copious resin flow. They also state that resin flows are indicative of decline of the host and that such trees usually die within a relatively short time.

Effects on Woods

In time, the wood of ponderosa pine infected by dwarfmistletoe becomes pitch-soaked and brashy. There in excess ray parenchyma, but detailed studies of the infected wood have not been made. Wellwood (1956) noted that sapwood of western hemlock infected with *Arceuthobium campylopodum* had a lower specific gravity and lower moisture content than uninfected wood. Preliminary tests with ponderosa pine suggest that infected sapwood has a lower moisture content but a higher specific gravity than uninfected wood (table 2). Statistical tests indicate that the differences between infected and uninfected wood are all highly significant. In the older sample tested, the moisture content in the infected part was about one-third that in uninfected parts of the same stem. The marked increase in specific gravity in the older sample is thought to be a result of extensive resin infiltration which is characteristic of old infections.

TABLE 2.—*Comparative specific gravity and moisture content of wood infected by dwarfmistletoe and adjacent uninfected wood in the same ponderosa pine tree, Fort Valley Experimental Forest, Ariz.*

Type of wood	Annual rings in sample	Determinations	Moisture content, mean and standard error	Specific gravity,[1] mean and standard error
	Number	*Number*	*Percent*	
Tree No. 1:				
Uninfected	15	3	158±1	0.41±0.01
Infected	15	3	116±4	.46± .01
Tree No. 2:				
Uninfected	35	5	122±4	.51± .01
Infected	35	5	38±6	.81± .03

[1] Ovendry weight, ovendry volume basis. Samples from lower boles of 70-year-old trees.

FACTORS INFLUENCING THE DISTRIBUTION OF DWARFMISTLETOE

Characteristically, dwarfmistletoes are irregularly distributed, and their abundance even in adjacent stands may vary considerably. In this section, some of the factors that influence the distribution of the parasite in Southwestern ponderosa pine forests are discussed. An important factor to keep in mind is that spread of dwarfmistletoe is slow. The return of the parasite into areas where it has once been eliminated is a longtime process. The reason is that the seeds are not disseminated by wind and, with the exception of occasional long-distance spread by birds, the spread is decidedly local. The slow spread of dwarfmistletoe is perhaps nowhere better illustrated than in the volcanic area northeast of Flagstaff, Ariz. Here, approximately 900 years ago, an eruption covered an area of about 100 square miles with a layer of cinders and ash deep enough to kill the forest cover. Ponderosa pine has returned into the areas where it was once killed out, but there is very little dwarfmistletoe in these stands. The only infection present is along the edge of the cinder area. A survey showed that infected stands account for less than 1 percent of this ponderosa pine area compared with 37 percent infection on an adjacent ranger district where the volcanic activity occurred several thousand years ago.

The present distribution of dwarfmistletoe is the result of the slow spread of the parasite from infection centers over countless generations, with interruptions in its range in places where the host has been destroyed by fire, volcanic activity, or logging.

Type of Stand

The spread of dwarfmistletoe is most rapid from overstory trees to an understory and is considerably slower through even-aged stands. The two-aged ponderosa pine stands common in some parts of the Southwest present optimum conditions for the spread of the parasite.

The rate of spread of this species was measured in various types of stands as part of the present investigation, and it was found to average 1 to 2 feet per year (page 66). The results show that there are not only differences between overstory to understory and lateral spread through even-aged stands but also between stands of different densities. The parasite progressed about one-third more rapidly through open-canopied than through closed-canopied stands.

Stand History

Although the temporary destruction of the forest cover by volcanic activity has been a factor in checking the spread of dwarfmistletoe in a few local areas, it is of little significance on a regional basis when compared with the effect of destruction by fires and logging. Severe fires have probably been the most important factor in keeping dwarfmistletoe in check, for once large areas of ponderosa pine forests are killed, the spread of the parasite back into the area is considerably slower than the return of the pine.

Many early logging operations where clear cutting was approached had somewhat the same effect as severe fires. Many of these stands were mature ponderosa pine with little or no understory; thus, the removal of essentially all merchantable trees also eliminated the parasite over large areas. Notable examples of such cuttings are to be found in northern New Mexico and in central Arizona. Occasional patches of infection, where the trees were too small or too deformed to be harvested, confirm that the parasite was once considerably more widespread in these stands than at present.

Most of the logging done under various modifications of the selection system has tended to intensify dwarfmistletoe in the residual stands. This stimulation of the parasite in cutover stands is well known in the Southwest, and for other species of *Arceuthobium* elsewhere. It is presumably due to increased light, although improved host vigor of residual trees may also be an equally important factor. The removal of only heavily broomed trees is ineffective in reducing the parasite, because such trees are often the least important as far as ineffectiveness is concerned. Often they produce fewer mistletoe fruits than more vigorous trees, which may have fewer infections.

Site Factors

It has been suggested (Korstian and Long 1922) that dwarfmistletoe on ponderosa pine is primarily a problem associated with poor sites. Actually, there is no clear-cut relationship between site quality and occurrence of the parasite. It is found on poor sites as well as on some of the best. However, site quality is often underestimated, because of the presence of weakened and dying trees in heavily infected stands.

In the Southwest, most ponderosa pine stands, on the basis of Meyer's (1938) site classification, vary from classes III to VI, with the majority of stands in classes IV or V (Pearson 1950, p. 40).

Andrews and Daniels (1960) recently found that, for virgin ponderosa pine in Arizona and New Mexico, infected stands had slightly higher gross volumes than uninfected stands. This was true despite higher current mortality rates in the infected stands. It indicates that the difference between volumes in infected and in healthy stands was previously greater than at the time of the survey.

Topographic Position

A possible explanation for the early reports and widespread belief that dwarfmistletoe is primarily a problem associated with poor sites is the high frequency of the parasite on ridges. The commonly overlooked fact is that although the frequency of dwarfmistletoe is unusually high on ridges, such sites constitute only a relatively small part of a forest area and, of course, are of even less importance when volumes are considered. Detailed information is available on the incidence of dwarfmistletoe in relation to topographic position in the Mescalero-Apache Reservation, N. Mex. (Hawksworth 1959b). As shown in the following tabulation, the incidence of dwarfmistletoe in the ponderosa pine type was nearly twice as high on ridges as in bottoms, but 87 percent of the infected stands were on slopes. Eight percent of the infected stands were on ridges, and these contained only 4 percent of the total infected volume.

		Plots with dwarfmistletoe	
Topographic position	*Plot basis (number)*	*Basis (number)*	*Frequency (percent)*
Bottom	167	62	37
Slope	2, 146	1, 142	53
Ridge	151	101	67
Total or average	2, 464	1, 305	53

The explanation for the high incidence of the parasite on ridges is not known, but its presence there is not thought to be due simply to poor growing conditions. The reason for this belief is that dwarfmistletoe is exceedingly rare on other poor sites, for example, at the lower limits of the ponderosa pine type. It is possible that this high incidence may be due to high light intensity on the ridges, since dwarfmistletoes are reported to be very sensitive to light (Gill 1935, p. 216). MacDougal (1899) suggests that the high incidence of the parasite on ridges and along the rims of mesas might be due to higher relative humidity at these places as a result of ascending humid air currents.

Steepness of Slope

Roth (1954) found that on ponderosa pine on one locality in Oregon there was a marked increase of infection from *Arceuthobium campylopodum* f. *campylopodum* with increasing degree of slope. On the Mescalero-Apache Reservation, N. Mex., the incidence of *A. vaginatum* f. *cryptopodum* in the ponderosa pine type decreased as steepness of slopes increased, but the differences were relatively small (Hawksworth 1959b):

Steepness of slope	*Plot basis (number)*	*Plots with dwarfmistletoe* — *Basis (number)*	*Plots with dwarfmistletoe* — *Frequency (percent)*
Gentle (under 10 percent)	1, 092	618	57
Moderate (10 to 30 percent)	621	328	53
Steep (over 30 percent)	433	196	45
Total or average	2, 146	1, 142	53

Chi-square tests indicate that the difference between gentle and steep slopes is highly significant; between moderate and steep slopes, the difference is significant. The difference between gentle and moderate slopes is not significant. Similar results were obtained for this species from plots in the ponderosa pine type throughout Arizona and New Mexico (Andrews and Daniels 1960).

Elevation

Korstian and Long (1922, p. 2) report that in Arizona and New Mexico *Arceuthobium vaginatum* f. *cryptopodum* is most abundant near the lower limits of the ponderosa pine type, and Palmer (1929) records a similar observation in western Texas. However, this is not the case; the parasite decreases in abundance with decreasing elevation and is exceedingly rare in the marginal ponderosa pine stands. The relationship between elevation and occurrence of the parasite within the commercial forests of the Mescalero-Apache Reservation, N. Mex., is shown in figure 14 (Hawksworth 1959b). Incidence was highest (60 percent of the plots with mistletoe) at the median altitude, and it decreased both at higher and lower altitudes. For the Southwest as a whole, frequency of this mistletoe increased with altitude, and no decrease at the higher elevations was noted (Andrews and Daniels 1960).

Aspect

Korstian and Long (1922, p. 3) indicate that ponderosa pine dwarfmistletoe is most abundant on south slopes. This was confirmed for the Mescalero-Apache Reservation, as the incidence on south and southwest slopes was 61 percent (plot basis), and on north and northeast slopes 46 and 44 percent, respectively (Hawksworth 1959b). The parasite was more common on gentle than on steep slopes on all eight major aspects. The highest incidence was on gentle, west slopes (74 percent) and the least on steep, northeast slopes (33 percent). However, Andrews and Daniels (1960) found no relationship between aspect and frequency of this parasite in their survey of all commercial ponderosa pine stands in Arizona and New Mexico.

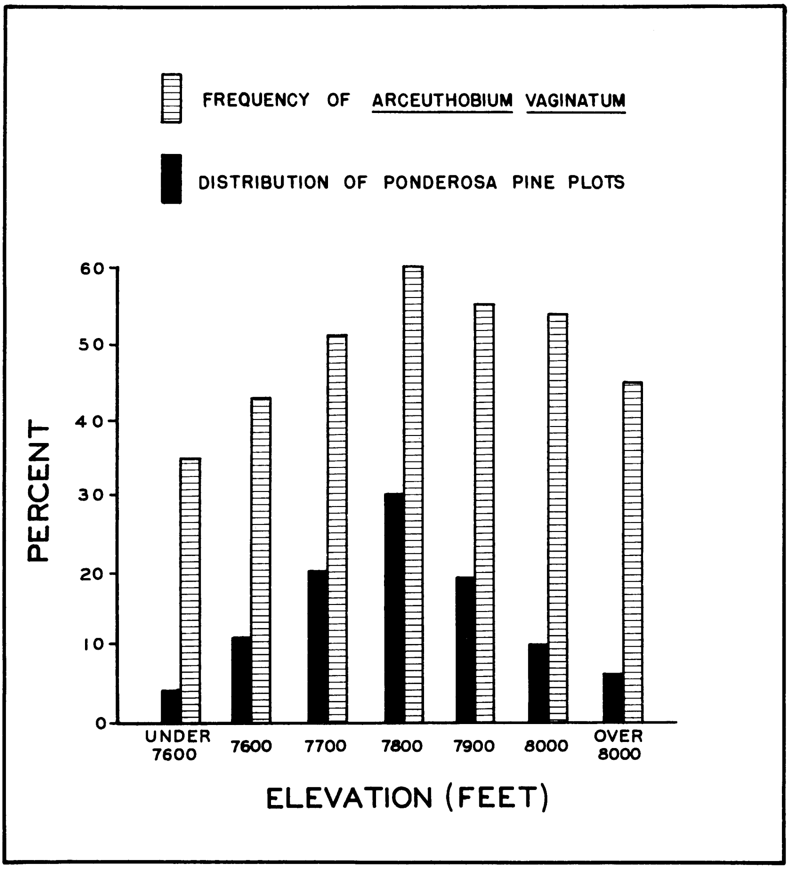

FIGURE 14.—Relationship between elevation and incidence of ponderosa pine dwarfmistletoe on the Mescalero-Apache Reservation, N. Mex. Basis: 2,146 plots.

CONTROL

Before direct control measures are discussed, mention will be made of natural factors that tend to reduce the incidence of infection. These are the occurrence of resistant trees and the activity of biological control agents.

Natural Control

Resistant Trees

Bates (1927) reported a slow-growing, straight-boled form of ponderosa pine in Colorado that was apparently well adapted to dry sites and in addition seemed to be nearly immune to dwarfmistletoe. Near-immunity was presumed because of the extreme scarcity of the parasite on this form of ponderosa pine. These trees were examined in 1959, and some were lightly to moderately infected. Tests are planned to determine the relative susceptibility of these trees and their progeny in comparison with ponderosa pine from other areas.

In ponderosa pine stands in the Southwest, as in most dwarfmistletoe-infected forests, there is a marked variation of amount of mistletoe in trees that have presumably been exposed to comparable amounts of infection (Gill 1935, p. 215). It is, of course, impossible to determine the amount of infection to which a certain tree has been exposed, but occasional instances are noticed that lend strong circumstantial evidence to the idea of susceptibility differences.

Two cases of presumed very low susceptibility, but none of complete immunity, have been observed in the Southwest. One of these was on the Grand Canyon National Park, Ariz., and the other on the Mescalero-Apache Reservation, N. Mex. In both cases, pole-sized trees with two infections each were surrounded by heavily infected trees bearing several hundred infections. The supposedly resistant trees were so close to the heavily infected ones that their branches intermingled. The four infections on the two presumably resistant trees were of very poor vigor, although the hosts were of good vigor. In three of these infections no shoots were present, but dissection swellings disclosed sinkers in the host branches.

Because of the manner in which dwarfmistletoe seeds are dispersed, infection is variable even where the parasite is abundant. Trees in dense stands tend to screen their neighbors from infection. Although differences in amount of infection may be due to variation in host susceptibility, it is only when these differences are extreme, as in the two cases just cited, that one can assume that this is probably a primary factor.

It is not known why trees are susceptible to dwarfmistletoe. Bates (1927) suggested that the resistance of trees he had studied was due to "lack of succulence" of the limbs of this particular form. Physiological factors are probably involved in resistant trees noticed in the Southwest, because there were no obvious morphological differences.

Biological Factors Affecting Dwarfmistletoe

Some biological agents destroy dwarfmistletoe shoots or seeds. However, none of the agents appear to be abundant or persistent enough to seriously reduce dwarfmistletoe populations, although they may be effective in certain years. Those agents that merely destroy shoots are not fatal to the dwarfmistletoe plant. The endophytic system of the parasite is not affected, and new shoots are soon formed.

Fungi

No parasitic fungi have been previously reported on *Arceuthobium vaginatum*. At least four species of fungi are known to attack dwarfmistletoes in the United States, and two of these are common in the Southwest on other species of *Arceuthobium*. *Wallrothiella arceuthobii* (Peck) Sacc. was seen in only one instance on *A. vaginatum* f. *cryptopodum* where a collection was made on the Mescalero-Apache Reservation in southern New Mexico. The few infected fruits on this mistletoe were found in a mixed ponderosa pine-Douglas-fir stand where *A. douglasii* on Douglas-fir was severely parasitized by the fungus. Because attacks of *W. arceuthobii* on *A. vaginatum* are so rare, this fungus cannot be considered of any importance on this host. It has been previously reported on the other four United States species of *Arceuthobium* (Gill 1935, p. 219).

Septogloeum gillii Ellis parasitized *Arceuthobium vaginatum* f. *cryptopodum* following artificial inoculations, but it has not been observed on this species in nature (Ellis 1946, p. 28).

Insects

A number of insects are associated with dwarfmistletoe, and some of these are very destructive to shoots in certain years. The losses of a great many of the seeds in artificial plantings suggest that insects are probably important in nature also. Thrips, which are presumably pollinators of this dwarfmistletoe, have previously been mentioned.

A spittlebug, *Clastoptera obtusa* (Say) (Cercopidae, Homoptera), is the most conspicuous insect on this species of mistletoe (Korstian and Long 1922, p. 34). It destroys entire shoots but is rarely abundant enough to be important except locally. Although the insect is widely distributed, it seems to be somewhat more abundant in Arizona than in New Mexico.

A plant bug, *Neoborella tumida* Knight (Miridae, Hemiptera), was described from *Arceuthobium vaginatum* f. *cryptopodum* at Estes Park, Colo. (Knight 1927, p. 42). This insect is common in Arizona and New Mexico and, although it is a plant feeder, it seems to be of little or no importance.

Larvae of the thickset hairstreak, *Mitoura spinetorum* (Hew.) (Theclinae, Lepidoptera), feed on *Arceuthobium vaginatum* f. *cryptopodum* shoots (Remington 1958). Although they can destroy entire clumps of shoots, they are too rare to be considered important. The larvae have been collected in only two localities in northern Arizona, but they are found occasionally on this species in Colorado. Other reported food plants of this larva are *A. campylopodum* f. *campylopodum* in California (Comstock and Dammers 1938), *A. campylopodum* f. *divaricatum* in Arizona (Garth 1950, p. 31), and *A. americanum* in Colorado (Remington 1958).

Larvae of at least three Lepidoptera are important shoot destroyers of this mistletoe: *Dasypyga alternosquamella* Rag. (Pyralidae) and *Gelechia natalis* Heinrich (Gelechiidae) in Colorado (Heinrich 1921) and an apparently undescribed species near *Peronea* (Tortricidae), tentatively identified by Dr. C. L. Remington, Yale University, from larvae collected in Arizona. The geographic distribution of the three species is poorly known. These insects mine out the larger shoots and also feed on the younger shoots and seeds. In some localities and in some years they are so abundant that the ground in infected stands is littered with dead shoots. This damage has been noticed in many areas in Arizona, New Mexico, and Colorado.

A red mite, an undescribed species of *Brevipalis*, is commonly found in the scales of *Arceuthobium vaginatum* f. *cryptopodum* shoots throughout the Southwest. The same mite is found on the dwarfmistletoes of Douglas-fir and pinyon pine, *A. douglasii* and *A. campylopodum* f. *divaricatum*, respectively, but it does no noticeable damage to any of these three mistletoes.

Other insects associated with ponderosa pine mistletoe include a geometrid larva, a gray weevil, and a black scale insect. They are relatively rare and have not been identified. Many other insects are found in dwarfmistletoe shoots, but since their occurrence is very irregular they seem to be casual visitors.

Another effect of insects on dwarfmistletoe is the killing of mistletoe-broomed branches by small bark beetles. The species have not been determined, but presumably they are the common branch bark beetles of genera such as *Pityophthorus* and *Pityogenes*. Often the only branches attacked in a tree are those infected with dwarfmistletoe. This activity varies from year to year, and it was unusually common in 1957 in northern Arizona. The killing of infected branches by the beetles has relatively little effect on dwarfmistletoe populations. Usually the branches with the oldest brooms are attacked; as previously mentioned, these are relatively low in infectiveness.

Mammals

Taylor (1935, p. 51) made an intensive study of the porcupine in the Southwestern forests and notes that dwarfmistletoe is its primary food in the fall months. Taylor also discusses the role porcupines may play in the dissemination of dwarfmistletoe.

Infected bark is commonly gnawed by rodents. Since much of the work is on twigs too small to support a porcupine, Abert squirrels may be responsible. These squirrels are common in most ponderosa pine forests, and they are important twig cutters.

Both mule deer and white-tailed deer seem to relish dwarfmistletoe shoots, and they frequently feed on them in fresh logging slash. Under natural conditions, relatively few shoots are within reach of these animals.

Birds

Although most genera of Loranthaceae are dependent almost entirely on birds for their dispersal, birds play a relatively minor role in the dissemination of *Arceuthobium*. The evening grosbeak (*Hesperiphona vespertina* (Cooper)) is the only bird actually seen feeding on ponderosa pine dwarfmistletoe fruits, and this was but a single observation. However, the common occurrence of voided seeds indicates that the eating of mistletoe seed by birds is not rare. The germination rate of such seeds seems to be very low. The number of infections resulting from bird-disseminated seed is not known, and these are only apparent when they develop in areas where the parasite was not previously present.

Artificial Control

The only method for reducing dwarfmistletoes is by pruning infected branches or killing infected trees. Satisfactory chemical control methods for these parasites have not been found.

Chemical

Although a number of chemicals have been tested on dwarfmistletoes, none has been found that will kill the root system of the parasite without damaging the host (Gill 1954). A great many herbicides will readily kill the aerial parts of the plants, but resprouting soon occurs. The chemicals tested on *A. vaginatum* f. *cryptopodum* are listed by Gill.[3] Even were a chemical found that could kill dwarfmistletoe without undue harm to the host, it probably would not replace the need for effective silvicultural reduction of the parasite. Chemicals that kill the shoots only might be useful in certain high-value stands, because repeated applications could prevent fruiting and spread.

Pruning

If trees are lightly infected and if no infections are near the main stem of the tree, pruning of infected branches will eliminate or reduce the parasite. However, since pruning is expensive and since pruned trees often harbor many latent infections, the operation is of limited usefulness. Unless it is conducted in conjunction with stand-improvement work, pruning is practicable only in certain high-value areas such as administrative sites, campgrounds, or recreational areas.

Perry (1922) suggested that pruning could be practiced in ponderosa pine stands to preserve enough trees to reseed areas that were to be cut heavily to control dwarfmistletoe. While he considered pruning to be a technically feasible method for saving certain trees, he questioned the economic possibility of the operation because of the then low stumpage values.

Gill (1954, p. 7) states that if shoots are apparent on a branch within 1 foot of the bole, the parasite is probably already established in the bole and cannot be eliminated by pruning. A general pruning rule given by Kimmey (1957, p. 10) for California species of *Arceuthobium* is that a branch is prunable if the distance from the bole to the closest shoot or swelling is at least twice the diameter of the branch. Shea (1957) suggests that for *A. campylopodum* f. *campylopodum* on ponderosa pine in Oregon, branches in which the swellings are at least 4 inches from the bole may be safely pruned.

In 1952, a study of 470 branches was begun on the Fort Valley Experimental Forest, Ariz., to provide more precise pruning guides for ponderosa pine infected with *Arceuthobium vaginatum* f. *cryptopodum*. The 6-year interim results suggest that Gill's (1954) "one-foot rule" is conservative except for large branches. By 1958, shoots had developed at the pruning wounds of 50 of the pruned branches. The relationship between branch diameter and distance between the bole and the closest shoot was as follows:

Branch diameter (outside bark)	*Greatest bole-to-shoot distance that left an infection in the bole*
(inches)	*(inches)*
Under 1.0	4
1.1–2.0	6
2.1–3.0	8
3.1–4.0	10

By adding 2 inches to these data as a safety factor, the following tentative pruning rule was developed. If shoots on branches under

[3] Gill, L. S. *Summary of chemicals tested for controlling western species of dwarfmistletoe* (*Arceuthobium* spp.). Third Internatl. Forest Disease Work Conf. Proc., pp. 18–25. Nov. 30–Dec. 2, 1955, Spokane, Wash. [Mimeographed.]

1.0 inch in diameter are not closer than 6 inches from the trunk, the infection may be removed by pruning the branch flush with the bole. For each 1 inch increase in branch diameter, the minimum safe distance is increased by 2 inches.

Experimental pruning of heavily infected trees at the Grand Canyon National Park, Ariz., in 1950 has resulted in improved vigor of the trees. These results were noted even in trees with as much as 75 percent of the live crown length removed (and an estimated 90 percent of the total foliage) and in trees that were already declining in the upper crown. Such severe pruning is not recommended as a general procedure, but these tests show that certain high-value trees, although heavily infected, can be saved by pruning.

Pruning in heavily infected groups should not be attempted, because the number of incipient infections present in such trees is usually high. For best results, only lightly infected trees should be pruned. The need for a second pruning will be lessened if two or three whorls of branches above the highest visibly infected branches are also removed (Gill 1954, p. 7).

Silvicultural Control

Silvicultural control of dwarfmistletoe is the only practical method of reducing the disease in ponderosa pine forests under extensive management. To be most effective, the control operations should proceed as follows (Gill and Hawksworth 1954, Hawksworth and Lusher 1956):

1. Removal of all infected overstory trees.
2. Removal or pruning of all infected trees in the understory.
3. Followup operations in all size classes.

The removal of all infected merchantable trees is currently practiced in only a few areas in the Southwest. Observations in cut-over stands emphasize that even lightly infected trees should not be left, because the parasite is stimulated in the residual trees and infection soon reaches serious proportions. If possible, it is best to avoid cutting in infected stands during the seed-dispersal period of the parasite (mid-July to mid-August) to prevent its undue spread.

The second step, treatment of infected trees in the understory, should follow the removal of the infected overstory by 3 to 10 years, depending on the age and amount of infection in the young stand. Work of this type has been conducted on 12,000 acres on the Mescalero-Apache Reservation, N. Mex. (Hawksworth and Lusher 1956). The average cost was $4.17 per acre, which amounted to about 15 percent of the average per-acre stumpage receipts. Axes and powersaws were used to fell infected trees of submerchantable size, and a limited amount of pruning was done.

Because dwarfmistletoe plants undergo a latent period of 3 to 5 years or even longer before shoots are produced, control operations should be repeated after about 5 years to eliminate infections that were previously overlooked. A third treatment after an additional 5 or 10 years may be necessary in stands that are very heavily infected. Once the parasite population has been reduced, a light treatment at each cutting cycle should keep it at an innocuous level.

Dwarfmistletoe control in lightly to moderately infected stands can be accomplished with relatively minor modifications in current cutting practices. The only additional work needed is in the treatment of infected parts of the understory. Control in heavily infected stands is presently difficult, for it is necessary to make drastic changes in current cutting practices, which involve relatively light cuts. Here, it may be necessary to remove nearly every overstory tree, but some of them may be saved by pruning. Fortunately, areas of such severe infection usually account for only a small proportion of the infected stands. Control in heavily infected stands in the Southwest is also handicapped, because planting cannot be done successfully in that region. When satisfactory artificial planting procedures are developed, it will be a relatively simple matter to control dwarfmistletoe in heavily infected stands by clear cutting, removing infected unmerchantable trees of all sizes, and replanting.

LIFE HISTORY OF DWARFMISTLETOE AS DETERMINED BY INOCULATIONS

A series of inoculations with *Arceuthobium vaginatum* f. *cryptopodum* was begun in 1950, with the following objectives in mind:

1. To determine the factors influencing germination of dwarfmistletoe seeds and the establishment of infection.
2. To determine the relative susceptibility of different aged internodes [4] of ponderosa pine.
3. To obtain information on the development of dwarfmistletoe plants, including length of time between germination and shoot appearance, flowering, and fruiting.

REVIEW OF PREVIOUS WORK

Apparently the first inoculation experiments with the dwarfmistletoes in the United States were those of Weir in the Northwest (Weir 1918). He lists two infections of a species reported as *Arceuthobium vaginatum* f. *cryptopodum* (*Razoumofskya cryptopoda*) from seed collected at an unnamed locality in southern Utah and grown on ponderosa pine of local origin at Priest River, Idaho. A number of discrepancies in the publication, however, make an interpretation of his results for this species very difficult. For example, the seeds are listed in the body of his table 1 (Weir 1918, p. 10) as sown in 1912, but the heading of this table states that they were collected in 1914. Also, the species of *Arceuthobium* and source of the seed are not listed for a number of the inoculations. Finally, the date of collection of *A. vaginatum* f. *cryptopodum* seeds in Utah is recorded as September 4 to November 14. This is questionable since these dates do not coincide with the seed-dispersal period of the species, which is from about mid-July to mid-August. In the light of these discrepancies, it is apparent that Weir's information given for *A. vaginatum* f. *cryptopodum* cannot be relied upon.

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[4] The term "internode" is used here to denote the annual growth of pine stems between the branch whorls rather than in its strict botanical sense for segments of a stem between points where successive leaves arise. An alternate term "interwhorl" is suggested by Kimmey (1954), but "internode" is retained here because of its current widespread usage in this broader sense in both forestry and botanical literature.

The first inoculations with dwarfmistletoe in the Southwest were made by W. H. Long in the Sandia Mountains near Albuquerque, N. Mex., in 1916. He inoculated a number of conifers with several Southwestern species of *Phoradendron* and *Arceuthobium*, including the dwarfmistletoe now known as *A. vaginatum* f. *cryptopodum*. Many of the seeds were lost shortly after planting. The inoculations apparently were not followed up, as no reports on the results were issued. The only record of this work is Long's original field notes. The study area is complicated by its subsequent development into a heavily used recreation area.

In 1955, a search was made for the inoculated trees. Only one tree, a Douglas-fir inoculated with *Arceuthobium douglasii*, was definitely identified. Identification of the inoculations with ponderosa pine dwarfmistletoe was complicated by the natural presence of the parasite in the area. One ponderosa pine was found that was probably a test tree. This tree had a single large broom that was 5 feet high and 8 feet across. The mistletoe plant was a male, and there had been no reinfection in the tree. No other infected ponderosa pines were present within about 70 feet.

Gill (1954) recorded some preliminary information on the development of *Arceuthobium vaginatum* f. *cryptopodum*, based on the 3-year results of the 1950 inoculations discussed here.

METHODS

Because little information has been published on inoculation methods used for the dwarfmistletoes, these methods will be described in some detail.

Host Plants

The pines used for the inoculations were saplings and small poles in natural stands. To facilitate examination, most inoculations were made on trees that were short enough so that the internodes on the main stem could be easily reached from the ground. Usually, the main stem was inoculated as well as a certain number of branches. Most of the trees were from 10 to 20 years old, although a few were older.

Seed Collection

Dwarfmistletoe seeds were obtained by placing severed [5] ponderosa pine branches bearing female plants with near-ripe fruits in large paper sacks. The closed sacks were left in the sun for about 15 minutes, which was sufficient time to stimulate expulsion of seed by the most mature fruits. Usually, only a small number of the fruits discharged their seeds during this period. While it is possible to obtain seeds by squeezing them out of near-ripe fruits, this method was seldom used because the germination capacity of such seeds is not known. Weir (1918, p. 4), however, states that "seeds are capable of germination some 2 weeks before they are normally discharged from the capsule."

[5] Branches bearing near-mature dwarfmistletoe fruits can best be removed with a saw or pruner rather than with an ax, since the jarring of the ax causes many fruits to expel their seeds.

Seed Planting

Dwarfmistletoe seeds collected from the sacks were placed in petri dishes and then planted within 1 to 4 days. Before being placed on the pine, each seed was picked up with a pair of tweezers and dipped in water momentarily. This brief treatment enabled the mucilagenous coating to imbibe water, become sticky, and hold the seed firmly in place. Weir (1918, p. 3) placed mistletoe seeds in water for several minutes and then picked up each one by sucking it against the point of a dropping pipette. This method has the disadvantage of being slower and more tedious than the one just described. Another disadvantage of soaking seeds before placing them on twigs is that such seeds, when dry, do not adhere as tightly to a twig as those that are dipped and quickly placed before their mucilagenous coats expand.

Seeds were planted at different points on a selected internode. Usually, this was at the base of a proximal needle fascicle, but if no needles were present on the internode, a needle scar or sterile scale at a certain distance from the node was used. Also, few plantings were made on recent and 1-year-old wounds. Most plantings were made in the first 2 weeks of August during the peak of the seed-dispersal period. They were usually checked for germination about 2 months later, and subsequent examinations were made annually, usually in July.

Location of Plots

The location of the plots and the number of seeds planted at each are shown in table 3. More than 9,000 seeds were planted in 530 trees during the 8-year period from 1950 to 1957. Inoculations were made in nine areas in three States: five in Arizona, three in New Mexico, and one in Colorado.

Results

The number of infections apparent by 1958 on each of the inoculation plots is shown in table 3. Probably all the infections from the 1950 planting and most of them from the 1952 planting had produced shoots by 1958. The more recent plantings have not been established long enough for many of the infections to produce shoots. Successful infection was 5.4 percent for the 1950 plantings, 0.0 for 1951, and 4.9 percent for 1952; the 3-year average for all plantings was 4.6 percent. Possible reasons for the markedly different results in the various plantings are discussed in the following sections. Several infections from the 1950 inoculations are shown in figure 15.

Results of the inoculations are presented in two categories: the first deals with factors influencing the establishment of the parasite, and the second gives information on the ontogeny of young dwarfmistletoe plants.

Factors Influencing Establishment

Because less than 5 percent of the planted seeds resulted in infection, it is obvious that factors affecting the germination and survival of the seeds and the ability of the hypocotyls to establish new infections are of great importance.

TABLE 3.—*Summary of data for the inoculation plots, and infections apparent by 1958*

Plot number [1]	Location	Planting date	Seeds planted	Infections apparent by August 1958 [2]	
			Number	*Number*	*Percent*
1	Fort Valley Experimental Forest, Ariz.	8/50	600	6	1.0
2	do	8/50	729	76	11.4
3	do	9-10/50	245	0	0
3	do	8/51	346	0	0
4	do	8/52	682	48	7.9
5	Mescalero Reservation, N. Mex.	9/52	372	0	0
6	Cibola National Forest, N. Mex.	8/53	1,392	0	0
			[3] 239	3	1.3
7	Roosevelt National Forest, Colo.	8/53	129	4	3.1
6	Cibola National Forest, N. Mex.	8/54	455	6	1.3
8	do	7-8/54	607	0	0
1	Fort Valley Experimental Forest, Ariz.	8/54	460	0	0
3	do	8/54	545	0	0
4	do	8/54	653	2	.3
9	do	8/55	567	0	0
9	do	8/56	928	0	0
9	do	8/57	340	0	0
	Total		9,289		

[1] Plots 1 and 3 are in uninfected stands; all others are in or adjacent to infected stands.
[2] The basis used is the number of seeds planted on branches that lived for at least 4 years after the date of inoculation.
[3] A replanting following heavy losses of the original planting caused by insects.

Germination

The plantings show that germination of *Arceuthobium vaginatum* f. *cryptopodum* occurs shortly after the seeds are expelled from the fruits. Most germination took place within 1 month after planting, and none occurred after 2 months. Germination for this species is in August or early September during the summer rainy season. For other species in the genus, germination in the spring is the common rule (Kuijt 1955, p. 588).

Information on climatic conditions at the Fort Valley Experimental Forest, Ariz., during seed dispersal and germination is given in the appendix. In the last half of August, for example, the mean maximum temperature was 76° F. and the mean minimum was 42°. Measurable rain fell on about one-third of the days and averaged 0.09 inch per day. The relative humidity was approximately 100 percent for an average of 8 hours each night during this period.

Highest germination noted for the planted seeds was 40 percent, which was recorded 1 month after the 1957 plantings. Since counts were not made at the same time interval after each year's planting, it is impossible to make direct comparisons of germination percent for the different years. The proportion of viable, germinated seeds remaining on the twigs decreased from about 40 percent 1 month after planting to only 10 percent 1 year later.

Agents responsible for the loss of germinated seeds were not determined; this is an important aspect that should receive further attention. Presumably, insects are involved to some extent since they destroy many seeds before germination.

In general, the number of seeds that germinated was highest for seeds placed on the most recent internodes and progressively less on

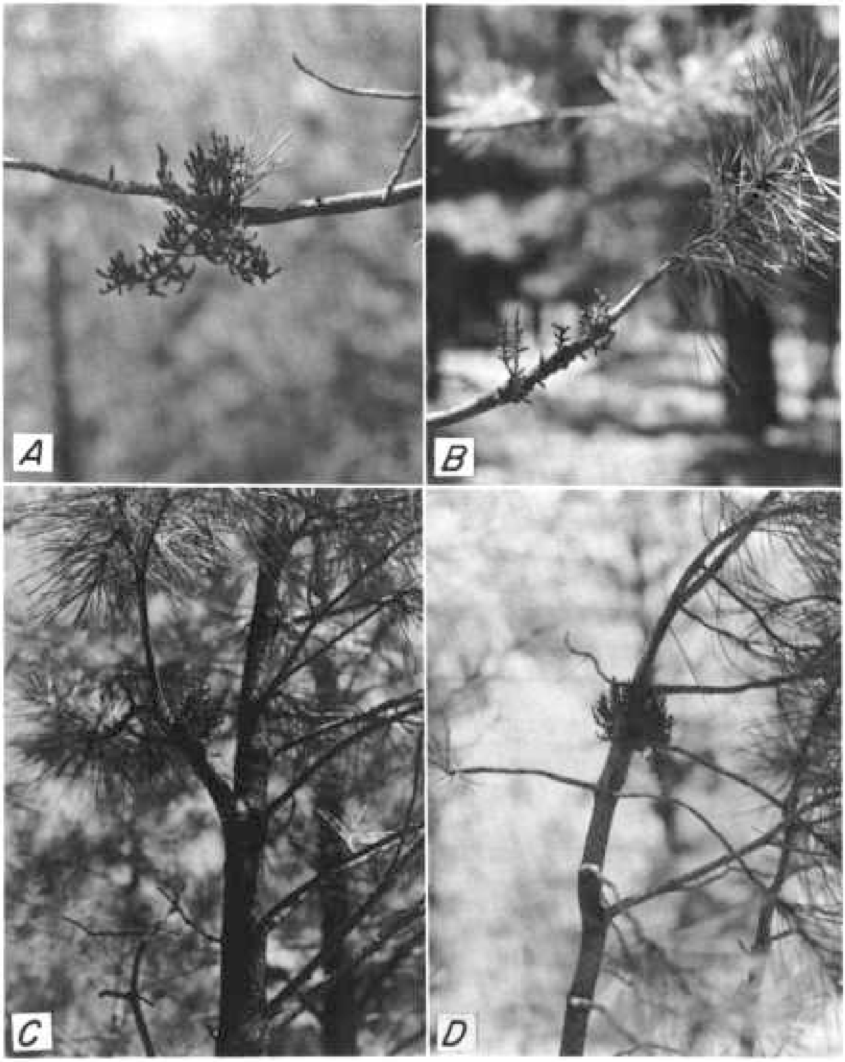

FIGURE 15.—Infections from the 1950 inoculations, photographed in 1957 on the Fort Valley Experimental Forest, Ariz. *A*, Shoots were first seen on this female plant in 1955. The tallest shoot in 1957 was 9.8 centimeters high. *B*, One of the few instances where infections developed on all three internodes inoculated. *C*, A female plant with shoots 9.8 centimeters high in 1957. Note the increased growth rate of the infected branch. *D*, A female infection on the main stem of a sapling.

older growth (fig. 16). It has been stated (Weir 1918, p. 4) that the reason for the lower susceptibility of older growth is lack of succulence, but results of this work suggest that seed losses may be equally important.

Length of time that a seed must remain in contact with the host to produce infection is not yet known, but is is probably at least 1 year.

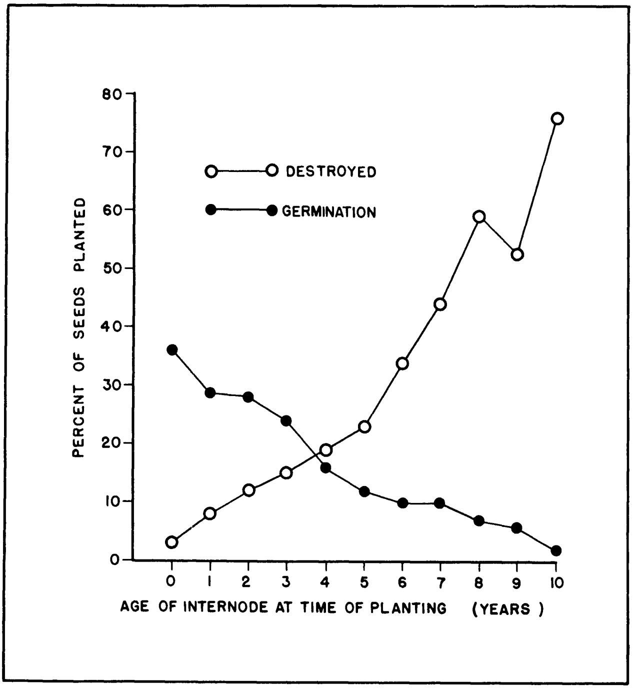

FIGURE 16.—Comparative germination and insect losses of seeds planted on different-aged internodes. The internode marked "0" indicates the current year's growth at the time of planting. Based on 2,885 seeds of the 1954–57 inoculations on the Fort Valley Experimental Forest, Ariz.

Destruction of Dwarfmistletoe Seeds by Insects

For those plantings on which information is available, 26 percent of the seeds were destroyed in place and 43 percent were removed. Insects are suspected as the primary agents responsible for these losses, although it is possible that larger animals, such as birds or mice, may also be involved. Some seeds were also dislodged by heavy rains.

The insects that destroy dwarfmistletoe seeds have not been determined but apparently several different species are involved, since the type of damage varies. Some seeds may be entirely removed; others may have only a small part eaten away. Small holes typical of weevil work were found in some seeds, while others with essentially intact seed coats were hollowed out.

The loss of dwarfmistletoe seeds to insects was about the same for plantings in infected stands as for those situated a half mile away from areas of general infection. This suggests that the insects are associated with ponderosa pine and that they may not be specific to the parasite.

Ants are suspected of being responsible for at least some of the losses, since they were observed removing intact seeds from opened petri dishes. Several species of ants are commonly associated with ponderosa pine. When seeds were placed in jars containing colonies of three different species of ants, they were not eaten; however, the activity of confined ants is not necessarily indicative of their behavior under natural conditions.

Larvae of an undetermined species of Lepidoptera—a borer of dwarfmistletoe shoots—feed on seeds in jars. This insect may account for some of the seed destruction in the inoculations, but it is probably not the primary insect. Damage done by weevil-like insects is less common than that done by other types.

The proportion of seeds destroyed by insects varied with the age of the internode on which they were placed (figs. 16 and 17). Losses were progressively greater on older growth up to about the tenth internode and then they declined. This might be explained by the relative exposure of seeds placed on internodes of different ages. The youngest five to six internodes bear needles, so seeds placed on the twig at their bases are often difficult to find. Seeds placed on 6- to 15-year-old internodes are exposed because most of the needles have fallen and in addition the twigs are relatively smooth.[6] The bark is rougher on older growth and, since here the seeds were placed in the crevasses rather than on the bark plates, the seeds on such growth were relatively concealed.

In general, the losses from inoculations made in Arizona and New Mexico were about the same (50 to 70 percent of the seeds), but in one of the New Mexico tests, more than 90 percent of the seeds were destroyed or removed within 3 weeks after planting.

Age of Internode

When the inoculation work was begun, Weir's (1916, p. 8) results indicating that growth more than 3 years old is not susceptible to dwarfmistletoe infection were used as a guide. The 3 years' growth tested were the current year (1950), 1 year old (1949), and 2 years old (1948). It became apparent, however, that ponderosa pine growth older than the oldest tested might also be susceptible. Weir (1916, p. 8) found that the youngest internode was most susceptible. The results for the Fort Valley Experimental Forest inoculations confirmed this, because the amount of infection on 1950 growth was twice that on 1948 growth:

Host internode year, and age at time of inoculation in 1950 [1]	*Seeds planted (number)*	*Infections by 1958 (number)*	*Infections by 1958 (percent)*
1950—Current year	425	39	9.2
1949—1 year	415	25	6.0
1948—2 years	407	18	4.4
Total or average	1,247	82	6.6

[1] Combined results for plots in infected and uninfected areas.

The 10 youngest internodes were used for the 1952 Fort Valley inoculations, and inoculations were made later on growth as old as 20 years. The results from the latter are not yet available, but those for 1952 show that all 10 internodes tested that year are susceptible:

[6] See figure 15, *A*; the internodes on twig at the right margin of the photograph are about 10 years old.

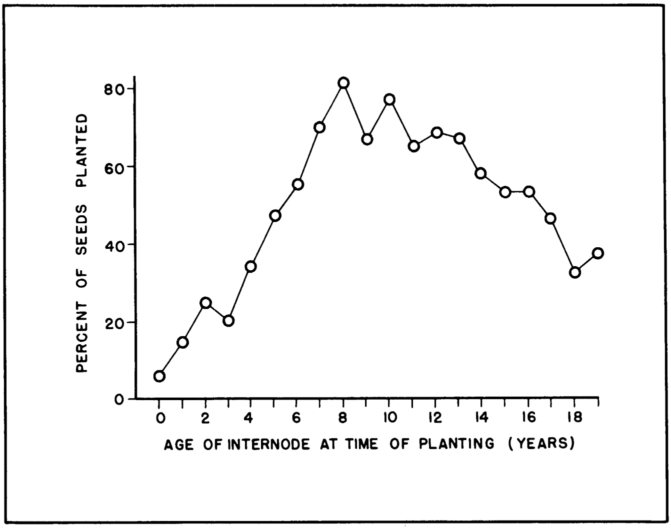

FIGURE 17.—Proportion of seeds destroyed by insects in relation to age of internode. Based on 902 seeds planted in 1956. Fort Valley Experimental Forest, Ariz.

Host internode year, and age at time of inoculation in 1952	*Seeds planted (number)*	*Infections by 1958 (number)*	*Infections by 1958 (percent)*
1952—Current year	56	6	11
1951—1 year	134	15	11
1950—2 years	57	6	9
1949—3 years	53	3	6
1948—4 years	57	2	4
1947—5 years	55	5	9
1946—6 years	56	4	7
1945—7 years	33	4	12
1944—8 years	56	1	2
1943—9 years	50	2	4
Total or average	607	48	7.9

These results also suggest that the more recent internodes are the most susceptible, although the results are more erratic than those in 1950, presumably because of the relatively small number of seeds planted on each year's growth.

Plot Location

The initial inoculations at Fort Valley were made in infected stands (area 2) and in stands where no dwarfmistletoe was seen (areas 1 and 3).[7] Plots in the infected and uninfected stands are about 1¼ miles apart and located on opposite sides of a treeless "park." The amount of infection resulting from the 1950 inoculation was 11 times as high in the infected stand as in the uninfected one:

[7] Mr. Francis R. Herman, formerly on the staff of the Fort Valley Experimental Forest, reports that there is a single infection about one-fourth mile west of this plot. The closest generally infected stands lie about one-half mile to the north of the plot.

1950 inoculations:	Seeds planted (number)	Infections by 1958 (number)	(percent)
Plot 1—Uninfected	585	6	1.0
Plot 2—Infected	662	76	11.4
Total or average	1,247	82	6.6

One plot, which was not inoculated until September and October, failed entirely. With this one exception, the inoculations were all made at the same time and with seeds from the same source.

The 1952 inoculations in the infected stand have resulted in 8 percent infection. Results of the 1954 tests are inconclusive to date. Only 2 plants from 650 seeds have resulted in the infected stand, compared with none from 1,000 seeds planted in the uninfected stands. The later plantings in the infected stand are too recent to indicate what proportion of infection has taken place.

It is unlikely that the higher incidence of infection in the areas where the parasite was already present was due to natural or accidental infection. All infections developed at the point where the seeds were placed. Furthermore, there has been relatively little recent infection on the noninoculated branches of the test trees. However, to virtually eliminate the possibility of contamination, beginning in 1952 only test trees more than 70 feet away from visibly diseased trees were used.

The reason for the marked differences in infection in the stands on opposite sides of the treeless park is not known, but data recorded for the planted seeds suggest that the difference is not associated with germination but with survival of the germinated seeds:

		Uninfected stands		Infected stand
		Plot 1	*Plot 3*	*Plot 4*
Seeds planted Aug. 1954	No.	460	545	653
Seeds germinated Nov. 1954	No.	105	102	84
Do	Pct.	23	19	13
Seeds viable May 1955:				
Basis	No.	0	0	18
Proportion of germinated seeds	Pct.	0	0	21

Germination in the 1954 plantings was actually better in the uninfected stands than in the infected stand, but none of the germinated seeds survived.

Climatic differences between the two areas may be sufficient to limit establishment of the parasite in the area where it does not now occur. Unfortunately, no comparative, long-term weather records are available for the two areas. Measurements [8] obtained during the summers of 1953 and 1954 indicate that the storms are more frequent in the area where the parasite is established. However, the total rainfall was about the same in the two areas.

The site quality on the two areas is similar, and both areas are on essentially level ground at about the same elevation. The soils on the two sites appear similar, although detailed studies have not been made.

[8] Information provided by Francis R. Herman, formerly of the Fort Valley Experimental Forest.

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The small number of infections resulting from inoculations in dwarfmistletoe-free stands is of interest. It indicates that ecologic or climatic factors are important in governing the distribution of dwarfmistletoe.

Time of Inoculation

Time of inoculation had a profound effect on degree of infection, since only plantings made in early August or late July were successful. No infections resulted from plantings made in late August, September, or October. Negative results were obtained from the late August plantings, even though they were made with seeds that had been dispersed naturally at that time. The September and October plantings were made with seed collected in August and stored indoors. Presumably, the importance of the time of inoculation is associated with the summer rainy season that makes conditions favorable for germination for only a short time.

Orientation on the Branch

In 1957, a tally of the infections developing from the 1950 inoculations was made to determine their orientation on the branch. The seeds had been placed at random around the twig at the base of the proximal needle in the internode. Twenty-four infections produced their first shoots late enough so that the original point of infection could be determined. A year or two after shoots appear, they are commonly formed on all sides of the branch so that it is no longer possible to detect the original point of infection, at least macroscopically. Of the 24 infections, 17 were in the lower quarter, 4 in the two side quarters, and 3 on the upper quarter.

The orientation of 294 natural infections was 80 in the top quarter, 116 in the lower quarter, and an average of 49 on each of the 2 side quarters.

Probably at least three factors influence the unequal distribution of infections around a branch. In the first place, since dwarfmistletoe seeds are expelled in an upward direction, the chances of a seed striking the underside rather than the upperside of a branch are greater. However, this would not account for the higher proportion of infection on tops of branches than on the sides. It seems possible that rain and hail are responsible for the removal of seeds from the sides; they may be either knocked off the branch or washed to the lower side. The common occurrence of infections on the lower sides of low branches that have no seed source below also suggests that some seeds may be washed to the lower surfaces. A third factor that may be involved here is that seeds on the upper parts of a branch may be killed by excessive insolation. The proportion of main-stem infections was higher on north than on south sides both in the inoculation tests and in natural populations. This would seem to indicate further that insolation may be a factor in determining where infection takes place.

Comparative Susceptibility of Various Trees and Tissues

Results from the 1950 inoculations suggest that there is no difference between susceptibility of branches and leaders. The amount of infection on the branches was 6.8 percent; on the leaders, 5.2 percent.

The percentages of successful infection was about the same for trees that were previously infected (10.3 percent) as for those that were not (11.8 percent). It has been claimed (Heinricher 1916) that for the European mistletoe *Viscum album* L. on pear, an initial infection lowers the susceptibility not only of the branch bearing the first infection but of the entire tree as well. However, this sensitization of pear by *V. album* is questioned by Paine (1950), and the results of this study suggest that there is no sensitization of ponderosa pine by dwarfmistletoe.

No infection took place through recent or 1-year-old bark wounds.

Ontogeny of Dwarfmistletoe Plants

Knowledge on the length of time between infection and shoot appearance is of primary importance in timing dwarfmistletoe control operations. Information on how soon mature fruits are produced is also of obvious practical importance.

The following discussion on the development of dwarfmistletoe plants is based on results of the 1950 and 1952 inoculations and a few supplemental studies of natural populations. The more recent plantings have not been established long enough to yield such information.

Swellings

Swellings at the point of infection usually precede the initial production of shoots and, hence, provide a means of detecting incipient infections. Results of this study, however, indicate that the time lapse between the development of swellings and first shoots is variable. In 52 percent of the infections, no swellings were noticed 1 year before shoots were first seen. However, swellings developed later so that by the time shoots appeared they were present in nearly all cases. Twenty-nine percent of the infections produced swellings 1 year before shoot appearance, and 18 percent 2 years before. In 1 percent, 3 years elapsed between the time a swelling was detected and the first shoots were seen. The few instances where no swellings were apparent, even after shoots had been produced, were mostly for infections on the main stem. As a rule, swellings were most pronounced on the smaller twigs where they were sometimes twice the diameter of the branch. The swellings are asymetrical at first but soon become regularly fusiform.

Shoots

Time of Initial Appearance

In the dwarfmistletoe infections resulting from the 1950 inoculations, shoots were first seen 26 months after the date of planting. However, shoots from most of the infections first appeared during the third, fourth, and fifth years after planting (fig. 18). It is assumed that most of the infections that resulted from the 1950 plantings had produced shoots by 1958, since only one new infection was noted in the 1958 examination. One-fourth of the infections first produced shoots in the third year after the date of planting, and about one-third in each of the fourth and fifth years, making a total of about 92 percent for these 3 years. It is, of course, possible that more infections will appear from this planting, but they will be so few that they will have little effect on the overall results.

Shoot appearance for the 1952 inoculations will apparently be similar to that of the 1950 plantings, although only 6 years' results are available for the later series. No shoots were seen in the first or second years after planting; 16 in the third, 15 in the fourth, 11 in the fifth, and 2 in the sixth.

Infections on the most recent internode tended to produce their first shoots sooner than on older growth. For example, in the 1950 inoculations, shoots appeared within 4 years on 78 percent of the infections on growth of the current year. Comparable figures for 1- and 2-year-old internodes were 38 and 44 percent, respectively.

The low proportion of successful infection from the 1950 inoculation in an uninfected stand has already been mentioned. An additional difference is that shoots appeared 4 years later in the uninfected than in the infected area.

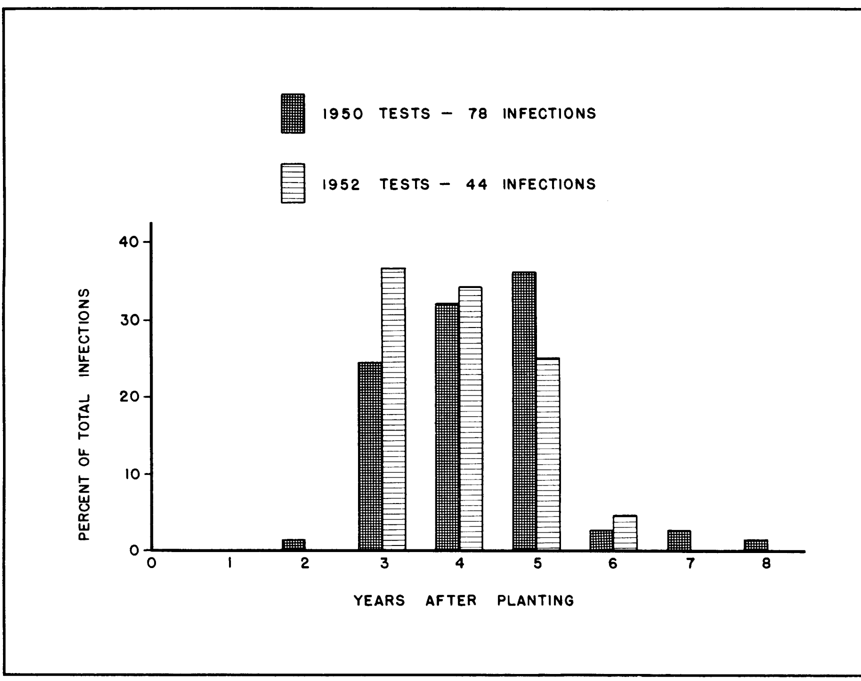

FIGURE 18.—Time of initial shoot appearance after the year of planting. Based on the 8-year results of the 1950 inoculations, and on the 6-year results of the 1952 tests. Fort Valley Experimental Forest, Ariz.

Growth Rate

Measurements of the tallest shoot in each infection were made periodically on eight dates between 1955 and 1958 to determine rate of growth. Most of the following information on annual growth is based on readings taken in late July or early August. Shoot height increased rapidly for 3 years after appearance and then leveled off or declined slightly (fig. 19). During the first 3 years the shoots grew an average of 1.5 centimeters per year. Reasons for the decline in average growth rate after 3 years include (1) shoot destruction by insects, rodents, and other agencies, (2) shortening of the shoots due to natural shedding of flowers and fruits, and (3) decline in shoot growth rate as the peak period of active growth is passed. This decline is shown in figure 20 and in the following tabulation of yearly height growth of infections from the 1950 inoculations:

	Annual shoot growth		
	1955–56 (*cm.*)	*1956–57* (*cm.*)	*1957–58* (*cm.*)
Unmolested infections [1]	3. 2	1. 9	1. 1
All infections	1. 2	. 5	0. 0

[1] Infections that were not noticeably affected by insects, rodents, deer, or other agencies.

As might be expected, little shoot growth occurred during the winter months. Only slight increases were recorded between October

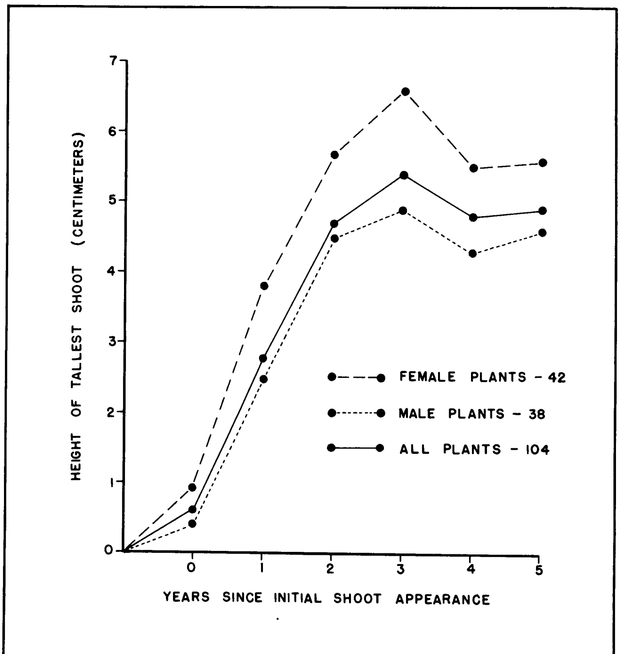

FIGURE 19.—Height of tallest shoot in each infection in relation to time since initial shoot appearance. Based on infections from the 1950 and 1952 inoculations. Fort Valley Experimental Forest, Ariz.

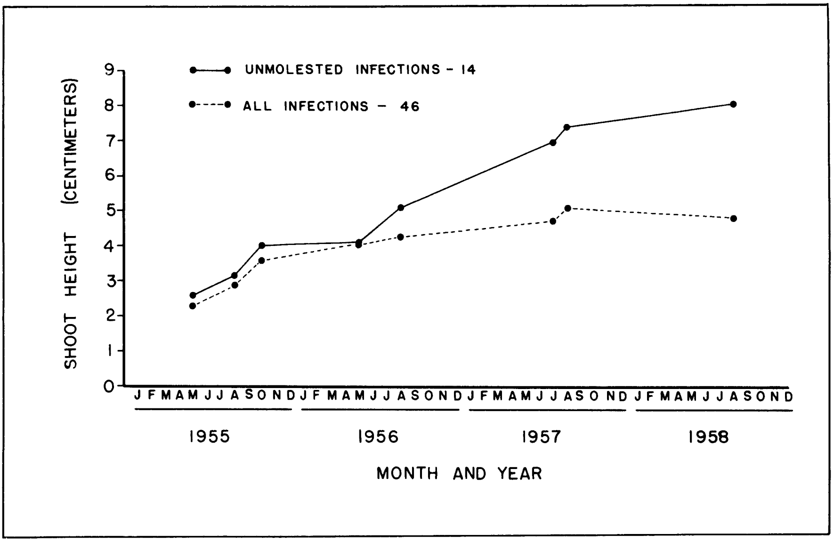

FIGURE 20.—Height of shoots from the 1950 inoculations at various times from 1955 through 1958. The number of shoots used as a basis for each curve is shown in the legend. Fort Valley Experimental Forest, Ariz.

1955 and April 1956 (fig. 20). The tallest shoot that developed by 1958 was 15.2 centimeters in a plant from the 1952 tests.[9] The maximum growth rate measured was 8.6 centimeters per year.

Female plants grew faster than male plants (fig. 19). In the infections from the 1950 tests, unmolested female plants grew 8.1 centimeters between 1955 and 1958, while comparable male plants grew only 3.7 centimeters.

Longitudinal Extension of New Shoot Formation

During the first 3 years after initial shoot appearance, the distance between the proximal and distal shoot increased from 1 to 2 centimeters per year, or ½ to 1 centimeter per year in each direction from the point of infection.

More detailed information on the annual rate of spread of dwarfmistletoe shoots was obtained in a supplemental study of 104 mainstem infections (table 4). The trees were felled, and the distance between the highest and lowest shoots was measured. Each stem was then dissected at the oldest point of infection; the age of the oldest ring with evidence of sinkers or growth stimulation was considered to be the length of time the parasite had been present. The relative rate of spread in dominant trees was nearly twice that in suppressed ones. The spread downward from the point of infection was 1.4 times greater than the upward spread.

[9] The tallest shoot seen in the Southwest for this species was 27.0 centimeters on the Sitgreaves National Forest, Ariz. The next two tallest plants measured in the region were 24.2 centimeters on the Fort Valley Experimental Forest, Ariz., and 21.5 centimeters on the Mescalero-Apache Reservation, N. Mex.

TABLE 4.—*Annual rate of spread of dwarfmistletoe shoots up and down the main stem of trees, by crown class*

Crown class	Infections	Average age of stem at infection	Apparent average age of infection	Relative rate-of-spread ratio
	Number	*Years*	*Years*	
Dominant	15	25	13	1.9
Codominant	20	24	12	1.6
Intermediate	34	24	14	1.4
Suppressed	35	20	11	[1] 1.0

[1] Rate of spread in suppressed trees taken as unity.

Flowers and Fruits

Both female and male flowers were first formed in the fifth year, or about 57 months after inoculation. Most plants first produced flowers in the second year after shoots appeared:

Time between shoot appearance and initial flowering (years)	*Male and female plants producing flowers (number)*	*Male and female plants producing flowers (percent)*
1	14	20
2	40	57
3	13	19
4	3	4
Total	70	100

Initial flowering may, of course, be delayed even longer if the first shoots are destroyed.

Sex Ratio

Kimmey (1957, p. 4) in a general discussion of California species of *Arceuthobium* states that the female and male plants occur in about a 1:1 ratio. Of the 80 plants of *A. vaginatum* f. *cryptopodum* from the inoculations, in which the sex was apparent by 1958, 42 were female (52.5 percent) and 38 were male (47.5 percent). This indicated that a 1:1 ratio existed for this species also. A supplemental count of 1,000 natural plants was then made on the Fort Valley Experimental Forest, Ariz. Results of the count showed that 507 were female and 493 were male, thus confirming that a 1:1 sex ratio exists for this species.

Fruit Production

The first mature fruits were produced 6 years after inoculation, although on most plants they were first produced in the seventh year:

Time since inoculation (years)	*Infections with first mature fruits (number)*	*Infections with first mature fruits (percent)*
6	4	27
7	9	60
8	2	13
Total	15	100

The approximate number of fruits produced on these plants during the sixth, seventh, and eighth years was 216, 100, and 350, respectively.

Complete data were not available for the eighth year (1958), because the counts were not finished before the seed-dispersal period. The differences in average numbers of fruits are of little significance, because of the great variation (from 1 to approximately 1,000) in individual plants.

DWARFMISTLETOE SEED FLIGHT

The explosive fruit of *Arceuthobium* is one of the most efficient mechanical seed dispersal mechanisms of any of the higher plants (Ridley 1930, p. 663). *Korthalsella* is the only other genus in the family Loranthaceae that has explosive fruits. However, the distance seeds are expelled is much less for *Korthalsella* than for *Arceuthobium* (Sahni 1933).

The mechanism of the explosive fruits of *Arceuthobium* is not completely understood, as evidenced by the disagreement among those who have worked on the problem (Kuijt 1955, p. 587). The main point of dispute is how the great pressures are developed which result in ejection of the seed from the fruit. According to MacDougal (1899), this force, although not measured, probably exceeds several atmospheres. A brief account of the expulsion mechanism is given in the review section (p. 10).

Dowding (1929, p. 98) found that the maximum horizontal distance traveled by artificially discharged *Arceuthobium americanum* seeds was 33 feet. For an unnamed dwarfmistletoe, Weir (1918, p. 34) records a horizontal seed flight of 66 feet from a point 8 feet above the ground level. The average distance of seed flight for *A. vaginatum* f. *cryptopodum* was given by MacDougal (1899) as 2 to 3 meters and by Gill and Hawksworth (1954) as about 15 feet. The average horizontal distance observed for natural discharge in the present study was 17.4 feet, with an extreme of 42.0 feet.

The distance of seed flight from an overstory tree to reproduction is frequently greater than the distances of seed flight cited, because (1) the influence of wind is a significant factor in the distribution of the seed of some species, and (2) some seeds still have a marked horizontal-force component even after they fall below the level of the point of discharge.

Roth (1953) found that for *Arceuthobium campylopodum* f. *campylopodum* on ponderosa pine averaging 120 feet tall in Oregon, infected reproduction extended 130 feet in the direction of the prevailing winds. Weir (1916, p. 34) mentions an extreme case where the seeds of *A. campylopodum* f. *laricis* were carried for one-fourth mile by winds. Studies by Gill and Hawksworth (1954) and further work reported here (p. 72) show that the infection patterns of *A. vaginatum* f. *cryptopodum* in Southwestern ponderosa pine are roughly circular; this suggests that prevailing winds are of little importance in the distribution of f. *cryptopodum*.

HORIZONTAL DISTANCE OF SEED FLIGHT

The objective of this part of the study was to determine the horizontal distance of seed flight to a point on the same level as the point of discharge.

Methods

Ponderosa pine branches bearing dwarfmistletoe plants with mature berries were cut and put immediately in cans of water; they were used in the seed dispersal studies only on the day they were cut. Care was taken to orient the cut branches in the position in which they were growing in the tree. The cans were placed on the ground next to an area covered with cardboard. This area was a 20° sector that extended for 50 feet (fig. 21). Because the study area was located in a stand where no dwarfmistletoe was present, all seeds found on the cardboard were from the test plants. There was little, if any, wind during these tests.

Results

Based on data for six dwarfmistletoe plants, the maximum distance of seed flight was 42.0 feet, with an average of 17.4±1.0 feet. As distance from the seed source increased, the number of seeds decreased steadily (fig. 22). The number of seeds per square foot in the 0- to 5-foot zone was 30 times that in the 30- to 35-foot zone and nearly 300 times that in the 40- to 45-foot zone. In figure 22, the actual number of seeds as well as the logarithm of the number of seeds is plotted over distance from the seed source. The linear regression line for the logarithmic data is highly significant (correlation coefficient = −0.96).

Angle of Discharge

Since the angle at which the seed is discharged has a marked influence on the distance of horizontal flight, an attempt was made to determine the average vertical angle of discharge.

Methods

Ponderosa pine branches bearing mature dwarfmistletoe fruits were placed in a plastic hemisphere that was about 45 inches in diameter. The inside of the hemisphere was lined with a 1- to 2-inch layer of cotton padding to catch the discharged seeds. Care was taken to orient each branch in the position in which it was growing when cut. The angle of discharge was measured with a specially built protractor (fig. 23). This work was done in the Roosevelt National Forest in northern Colorado.

Results

The average angle of discharge of 553 seeds was 30°±1.2° above the horizontal. For 18 mistletoe plants on branches, the angle was 40°±1.6° (317 seeds) compared with 15°±1.6° (236 seeds) for 2 on the main stem. Further studies are needed to determine whether the differences between branch and bole infections are consistent.

Preliminary results obtained with an earlier version of the apparatus shown in figure 23 indicated a higher angle of discharge for this species. Information was obtained on only eight seeds on the Fort Valley Experimental Forest, Ariz. The angle of discharge ranged from 50° to 81° above the horizontal with a mean of 67°±3°.

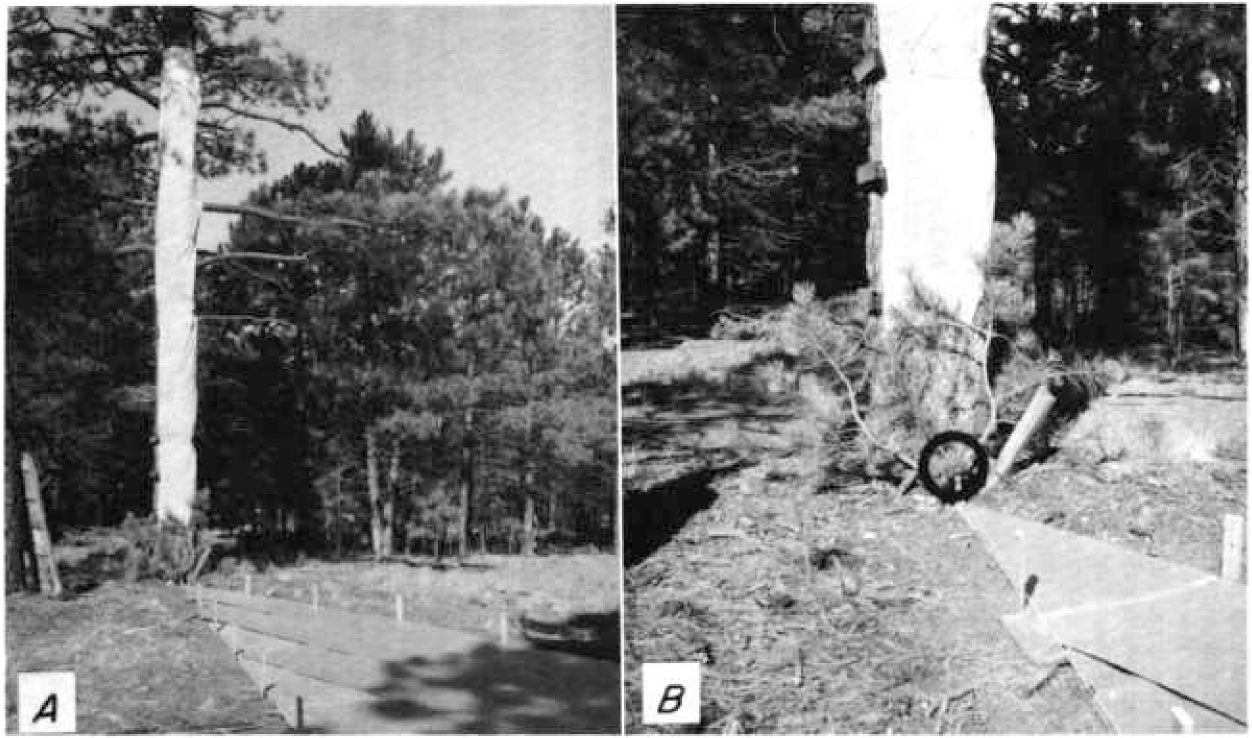

FIGURE 21.—Setup used to study the horizontal and vertical distance of seed flight. *A*, General view showing the 20° sector covered with cardboard for measurement of horizontal seed flight, and a strip of muslin on the bole of the pine to catch seeds shot directly upward. *B*, A ponderosa pine branch bearing mature dwarfmistletoe fruits (circle) in place at the base of the sector. Fort Valley Experimental Forest, Ariz.

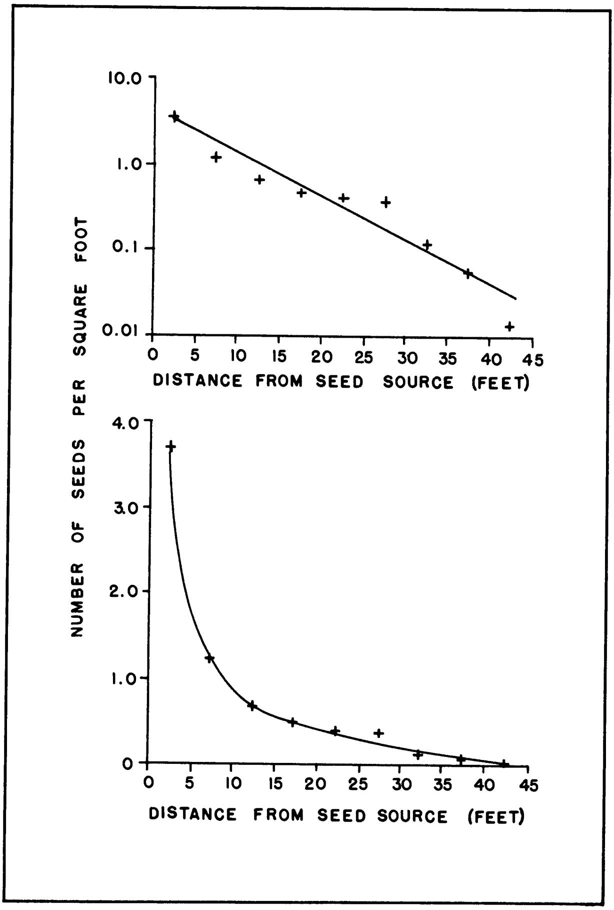

FIGURE 22.—Number of seeds per square foot at various distances from the seed source. The lower curve shows the actual number of seeds, and the upper one shows these same data plotted logarithmically. Basis: 109 seeds.

The reliability of the results of the Colorado and Arizona studies is discussed further in the following section.

TRAJECTORY CURVES

The objectives here were (1) to determine the distance of seed flight of dwarfmistletoe seeds expelled at a given angle, and (2) to construct a seed trajectory curve for the species.

A 45° angle of discharge was used, because it is the angle that gives the maximum horizontal flight distance to a point on the same level as the point of discharge. This angle does not give the maximum horizontal flight for points below the level of the point of origin. However, once the trajectory for a given angle is determined, the trajectory for any other angle can be easily calculated.

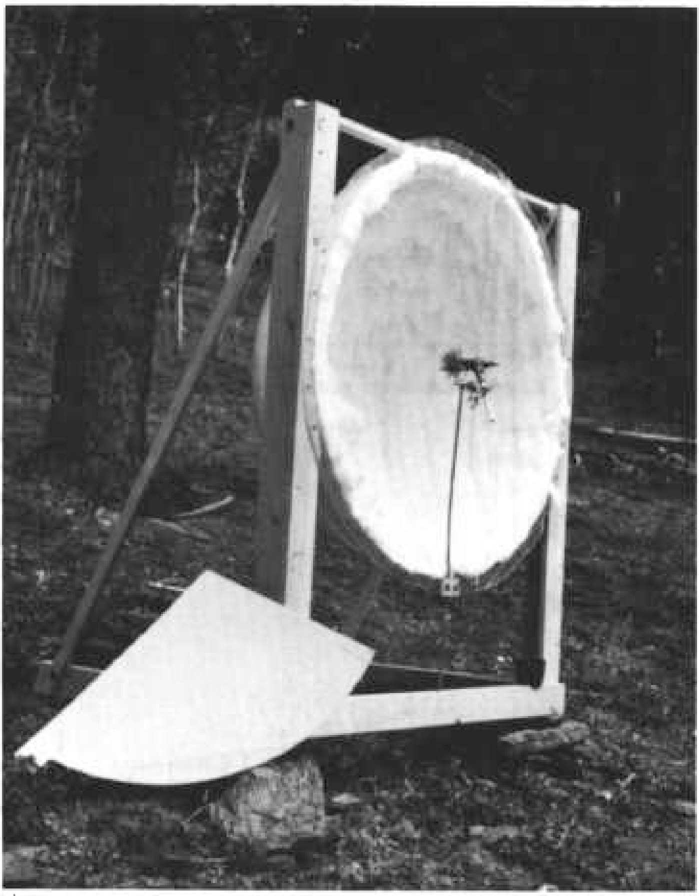

FIGURE 23.—Setup used to measure the angle of discharge of dwarfmistletoe seeds. The plants bearing mature fruits were fastened to the clamp in the center of the hemisphere. The inside of the hemisphere was lined with cotton padding so that the seeds would stick to it. The protractor used to measure the angle is shown in the foreground.

Methods

As described earlier in this section, it was originally planned to use naturally discharged seeds. However, because naturally discharged seeds made it difficult to obtain sufficient basic data to meet the objectives of this phase of the experiment, the seeds were artificially discharged. By gently squeezing the mature fruit, the seeds were readily expelled in a manner similar to natural discharge. Artificially discharging the seeds in this manner enabled the direction of seed to be controlled. It is not believed that a serious variable was introduced by this procedure, since the maximum horizontal distance of seed flight was about the same for the two methods: 42.0 feet for natural discharge and 40.2 feet for artificial.

The 45° angle of discharge was accomplished by discharging the seeds through a narrow horizontal slit in a cardboard box. The length of the box and width of the slit were such that only seeds traveling at an angle between 42° and 48° escaped from the box. The 20° cardboard sector described on page 53 was used for these studies also. Data were obtained at two heights: at ground level, and at 33 feet above the ground. To minimize the effects of differences between individual mistletoe plants, approximately one-half of the fruits from each plant were used at each height. More than 300 seeds were discharged at each height, but only a small number of them was found on the cardboard. Many seeds were not expelled at an angle that would allow them to escape from the box, and others that did escape landed to the side of the test area. There was little or no wind during the tests.

Results

Seeds discharged at ground level (81 seeds) traveled an average horizontal distance of 28.9±0.6 feet while those expelled at a point 33 feet above the ground (47 seeds) averaged 34.9±0.9 feet.

The presumed trajectory of seeds expelled at an angle of 45° is shown in figure 24. Although the curve is based on only three points, these seem to be sufficient to indicate the trend of the trajectory. The trajectory of seeds expelled at a 45° angle was used to calculate the trajectories of seeds discharged at angles of 0°, 30°, and 67° from a point 50 feet above the ground. The manner of calculation was to assume that in each case when the seed had traveled for a given period of time, the vertical departure from the original angle of discharge would be the same. The calculated horizontal distance traveled by seeds discharged at various angles at ground level and 25 and 50 feet above the ground (fig. 25) are as follows:

Angle of discharge (degrees)	*Height of seed source above ground*		
	0 feet	*25 feet*	*50 feet*
67	18	20	20
45	29	35	35
30	27	41	43
0	0	38	48

Although the Colorado measurements indicated an average discharge angle of about +30°, the trajectories based on the Arizona work indicate higher average angles. For an angle of about 30°, average horizontal distances of about 27 feet would be expected (fig. 25). However, the average distance from the Arizona studies was only 17 feet, so an average angle of more than 60° might be expected there. On this basis, the average angle of +67° obtained in the very limited Arizona studies might be representative for the species in that area.

The trajectory curves (figs. 24 and 25) show that the horizontal force of the seeds is quickly offset by air friction, and the seeds soon fall nearly vertically. The direct relationship assumed by some authors (Kimmey 1957; Buckland and Marples 1952; Tubeuf 1919, p. 244) to exist between the height of the seed source and horizontal distance of seed flight is true only for seeds expelled at low angles.

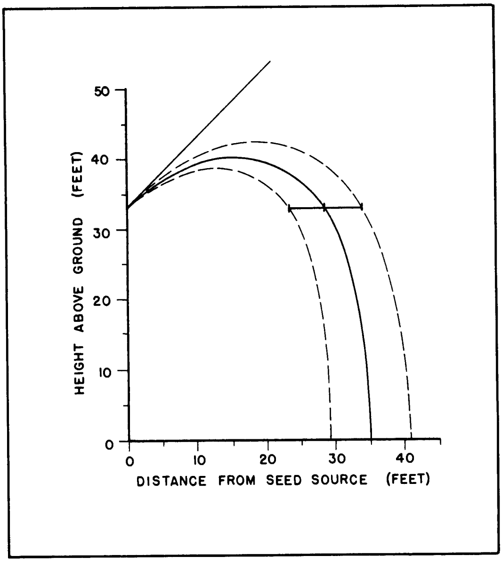

FIGURE 24.—Trajectory of seeds expelled at a vertical angle of 45°. The solid line indicates the average trajectory and the dashed lines represent plus and minus one standard deviation. Each curve is based on three points: the common point of origin, the horizontal distance of seed flight to a point on the same level as the seed source, and the horizontal distance of seed flight to a point 33 feet below the level of the seed source.

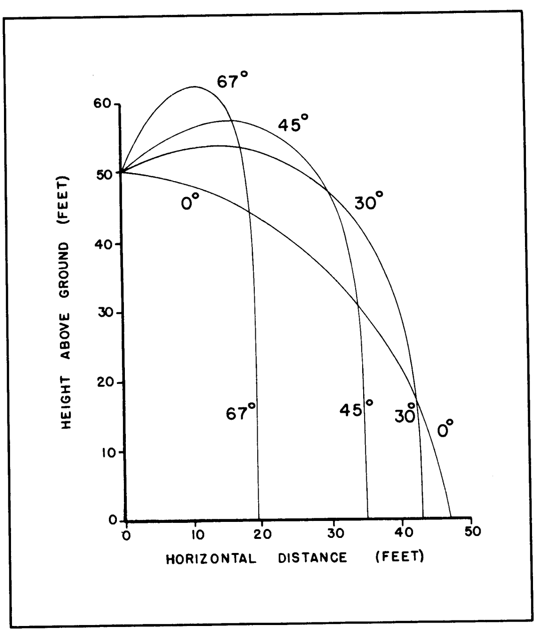

FIGURE 25.—Calculated trajectories of seeds expelled at four vertical angles from a point 50 feet above ground level.

The effect of height of seed source on the horizontal distance of seed flight is markedly reduced for angles of discharge over 45°. Height of seed source is also an important factor in the distribution of the dwarfmistletoes that are aided by winds.

BALLISTICS OF SEED FLIGHT

The dwarfmistletoe seed is oblong, somewhat conical on one end, and hemispherical on the other (the forward end in seed flight). The shape of the seed thus approaches the ideal for the most efficient projectile.

Some writers (Tubeuf 1919, p. 244; Dowding 1929, p. 99) state that the seeds in flight have a long tail of mucilage that trails from the pointed end and acts as a rudder. A quantity of viscous material is ejected from the fruit along with the seed, but that most of it remains attached to the seed is questionable. The liquid is scattered more or less at random. Immediately after alighting, seeds are coated (except for the base) with a thin semisolid layer of viscin. There is no liquid viscin present, which might be expected if masses of the material trailed behind the seed in flight. Even if the seeds do have a viscous tail as claimed, it is unlikely that this could be considered to favor seed flight. Such a tail would tend to decrease the horizontal distance of flight. Seeds leaving the fruit travel too fast to be observed by eye, so high-speed photography should be useful in settling this question.

After the seeds are slowed by air resistance, their orientation is changed from the round-end forward to a sidewise position. This is what would be expected for oblong, falling bodies as they approach their terminal velocity, and it was noted by Dowding (1929, p. 99) for the seeds of *Arceuthobium americanum*. Results of the present study also suggest this, since seeds that alighted with the hemispherical end (the forward end of the seed as it leaves the fruit) on the cardboard were observed only within about 20 feet of the seed source.

Determination of Initial Velocity

As far as known, no calculations on the initial velocity of dwarfmistletoe seeds or for any other species of higher plants with explosive fruits have been made. Buller (1933, p. 338) records rough estimates (disregarding air resistance) of the initial velocity of glebal masses of the fungus *Sphaerobolus stellatus*. This fungus expelled these spherical bodies, which are about 1 millimeter in diameter and weigh about 1 milligram, to a height of 14.5 feet indicating an initial velocity of at least 30 feet per second.[10]

A more precise determination of the initial velocity of dwarfmistletoe seeds was made by accounting for air resistance. This was calculated from measurements of heights of vertical seed flight and from experimentally determined rates of free fall (terminal velocity) of the seeds. A preliminary report on this work has already appeared (Hawksworth 1959a).

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[10] Based on the formula $V=\sqrt{2gH}$

when, V=initial velocity (feet per second)
g=acceleration due to gravity (32 feet per second^2)
H=height of vertical seed flight (feet)

Vertical Height of Seed Flight

The vertical height seeds will travel was determined by catching seeds shot directly upward onto a piece of muslin attached to the bole of a tree (fig. 21, p. 54). Severed ponderosa pine branches bearing mature dwarfmistletoe plants were placed at the base of the tree. These branches were the same ones used in determining horizontal distance of seed flight. Although this was not a precise method for determining the extreme height seeds will travel, it was simple and accurate enough for the present purposes. The results obtained are conservative, for the chances are very small that a seed would strike and stick to the muslin at the highest point in its trajectory.

The highest point reached by naturally discharged seed was 16.1 feet above the source, and the highest for those artifically discharged was 24.8 feet. It seems probable that if sufficient tests had been conducted with naturally discharged seeds, heights would have been considerably higher and approximately that of the artificially discharged seeds, because there was little difference in horizontal seed flight for the two methods. Heights for the artificially discharged seeds were probably greater because these seeds could be more easily directed toward the muslin; the naturally discharged seeds traveled in all directions and at many different angles.

Maximum vertical heights of about 20 feet would be expected. The maximum vertical height of a projectile expelled at an angle of 45° is approximately one-half of the horizontal distance covered. Since the average horizontal distance of flight for seeds expelled at 45° was 29 feet, the average vertical distance for these seeds when shot directly upward would be about 15 feet. A height of 15 feet was also determined when the trajectory of a seed shot directly upward was calculated as in figure 25.

Terminal Velocity of Seeds

The terminal velocity of dwarfmistletoe seeds in free fall was determined by placing them in a vertical tube through which air was passed upwards at a velocity just sufficient to support them. A plastic tube about 1 centimeter in diameter and 3 feet long was used. Air was blown into the bottom of the tube, and its velocity was regulated by a needle valve. As it left the top of the tube, its velocity was measured with a Hastings electrical air meter. The air speeds necessary to suspend 24 dwarfmistletoe seeds ranging in weight from 0.8 to 3.0 milligrams were determined twice for each seed and averaged (fig. 26).

From a random sample, the weight of 25 dwarfmistletoe seeds was estimated shortly after they were expelled. It ranged from 1.7 to 3.7 milligrams and averaged 2.4 milligrams. Terminal velocity of seeds weighing 2.4 milligrams would be about 1,470 feet per minute or 750 centimeters per second (fig. 26).

Calculation of Initial Velocity

The main factors needed to calculate initial velocity (vertical height of seed flight, terminal velocity, and seed weight) have been given in the two preceding sections. There are, of course, other vari-

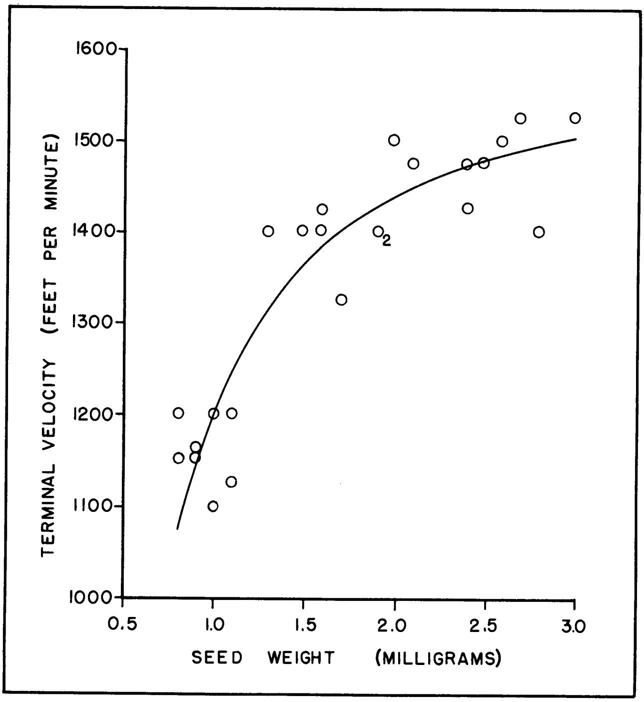

FIGURE 26.—Relationship between terminal velocity and dwarfmistletoe seed weight. Each point is an average of two determinations.

ables that have not been accounted for, such as differences in seed shape, and differences in air resistance due to altitude, temperature, and humidity. However, these would have only minor effects on the results, which at best can only be considered as approximations.

A curve (fig. 27) was calculated showing the relationship between the maximum vertical height that a seed will travel and the initial velocity necessary to attain this height. The formula used in this calculation is given in the appendix, page 109. It has been shown that dwarfmistletoe seeds will travel an average vertical distance of 15 feet. From figure 27 it can be seen that for seeds to be ejected to this height, an initial velocity of about 45 feet per second is necessary. Estimated initial velocities of seeds that traveled to greater heights are as follows:

Vertical height of seed flight	*Initial velocity per second (feet)*
16.1 feet (highest natural discharge)	48
21 feet (approximate vertical potential of naturally discharged seed that traveled for a horizontal distance of 42 feet)	58
24.8 feet (highest artificial discharge)	64

Other Ballistic Computations

The following calculations of dwarfmistletoe seed ballistics are based on an average initial velocity of 45 feet per second. Formulas and details for the calculations are given in the appendix, page 109.

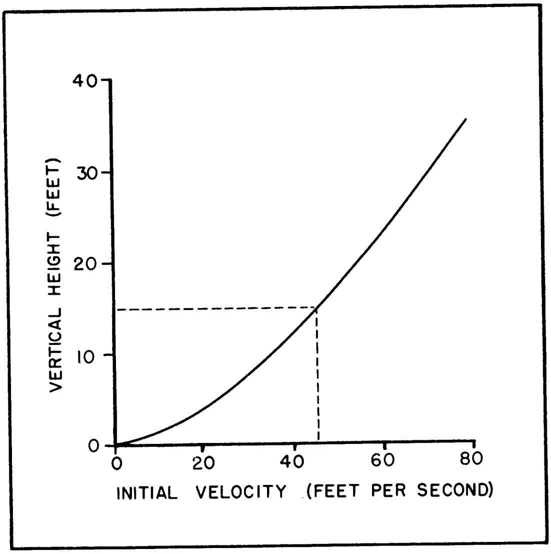

FIGURE 27.—Relationship between maximum vertical height of seed flight and initial velocity necessary to attain this height.

1. Seeds expelled directly upward reach the highest point in their trajectory in about 1.4 seconds, or 2.8 seconds for a complete flight back to the level of the point of origin.
2. It is estimated that seeds expelled directly upward reach their terminal velocity after falling about 10 feet.
3. The time taken for the seed to leave the fruit is estimated as $1/_{2300}$ second. Such a speed accounts for the fact that the actual act of expulsion cannot be seen by the unaided eye.
4. The kinetic energy of the seeds as they leave the fruit was calculated as 2.3×10^{3} ergs.
5. The initial acceleration of dwarfmistletoe seed was estimated at 4.7×10^{6} cm/sec^{2}, or nearly 5,000 times gravity.

SEED DISPERSAL PERIOD

The objectives of this phase of the study were (1) to determine the length of the seed dispersal period of *Arceuthobium vaginatum* f. *cryptopodum;* (2) to measure the relative number of seeds produced each year in 1955, 1956, and 1957 in one locality; and (3) to attempt to correlate seed discharge with meteorological conditions.

METHODS

Seed counts were made on 30 traps located in two types of heavily infected stands on the Fort Valley Experimental Forest, Ariz. A trap (fig. 28, *C*) consisted of a 24- by 60-inch sheet of cardboard tacked to two 6-foot posts. The traps were left in place after the counts for the year were made, and new traps were placed on top of the old at the start of the next year's dispersal period.

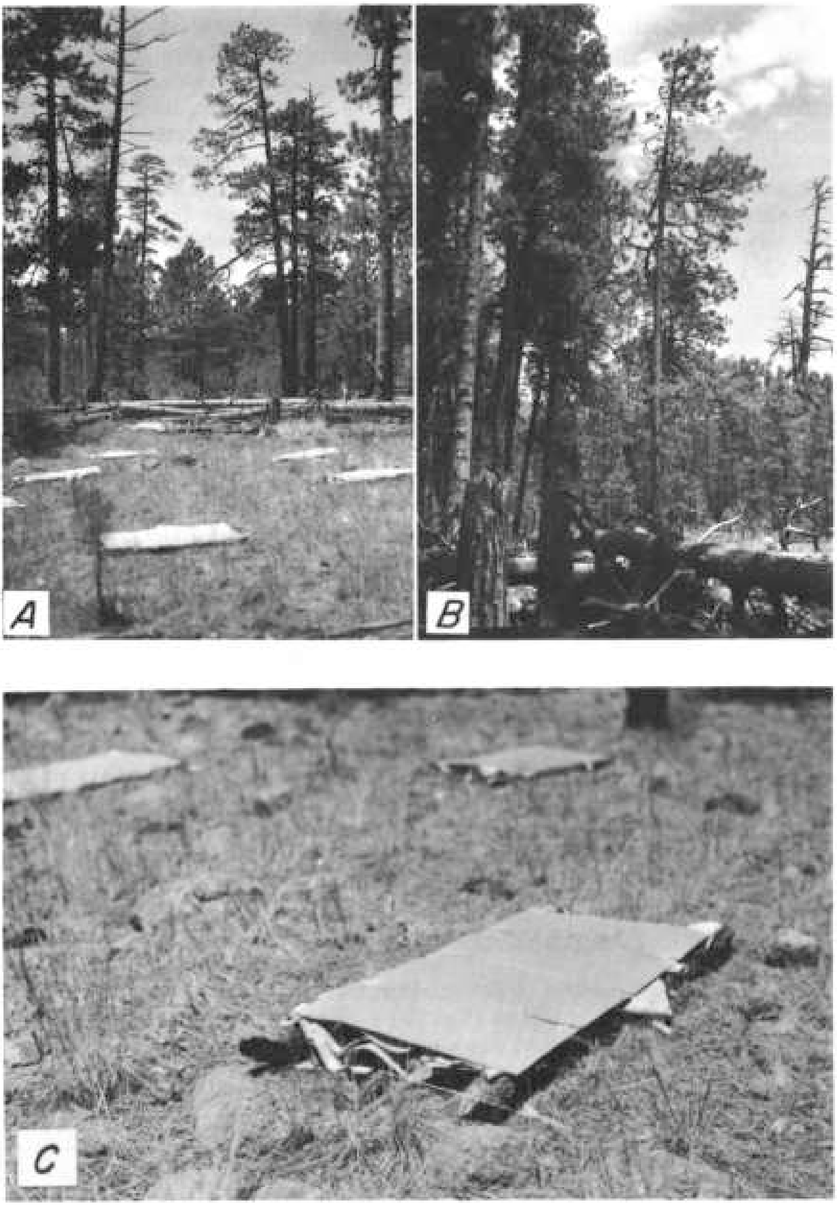

FIGURE 28.—Seed dispersal study area 2. *A*, General view of the area showing six of the seed traps in place. The heavily infected mature stand, which was the seed source, is to the right of the picture. Note the number of down trees killed by dwarfmistletoe. *B*, View of the infected stand. The seed traps are behind the down tree in the foreground. *C*, Closeup of one of the seed traps. Fort Valley Experimental Forest, Ariz.

The two locations selected for the seed trapping studies are on the check plots of the mistletoe-reduction study area of the experimental forest. Area 1 was located in check plot 2 in a 50-year-old, heavily infected pole stand. Twenty traps were placed here, including three under a mature ponderosa pine overstory rather than in the pole stand. Traps were distributed irregularly in small openings throughout one-half acre. Area 2 was located one-fourth mile south of area 1 in check plot 3. Here, 10 traps were placed in a one-tenth-acre opening adjacent to a heavily infected stand of mature ponderosa pine (fig. 28).

RESULTS

Number of Seeds Produced in 3 Different Years

Table 5 summarizes the number of seeds found on the seed traps during each of the 3 years of the study. The most were caught in 1956 (average 75 per trap), when the amount was 5 times that of the previous year (15 per trap). The number found in 1957 (31 per trap) was about twice that in 1955. The average for all 3 years was 40 seeds per trap (4.0 seeds per square foot).

Although differences in distribution of the seed traps do not permit a direct comparison between pole and mature stands, more seeds per trap were found in pole (average 62 per trap) than in mature stands (average 12 per trap). The variation of seed crop from year to year was markedly greater in pole stands (range, 19 to 120 seeds per trap per year) than in mature stands (range, 10 to 16 seeds per trap per year).

The number of seeds found on each trap during the 3 years of the study is given in the appendix, page 111. The extremes found on the traps in one season ranged from 1 to 248 seeds. In general, the majority of the traps showed the most seeds in 1956, fewer in 1957, and the least in 1955.

Length of Seed Dispersal Period

There were only slight differences in the length of the seed dispersal period in the 3 years studied (fig. 29). Even though observation was not started until after seed dispersal had begun, it is believed that the

TABLE 5.—*Average number of seeds found on seed traps in two areas and in two stand types in 1955, 1956, and 1957, Fort Valley Experimental Forest, Ariz.*

Area or stand type	Trap basis	Seeds per trap in—		
		1955	1956	1957
	Number	*Number*	*Number*	*Number*
Area 1	20	17	105	41
Area 2	10	12	14	11
Total or average	30	15	75	31
Pole	17	19	120	47
Mature	13	10	16	10
Total or average	30	15	75	31

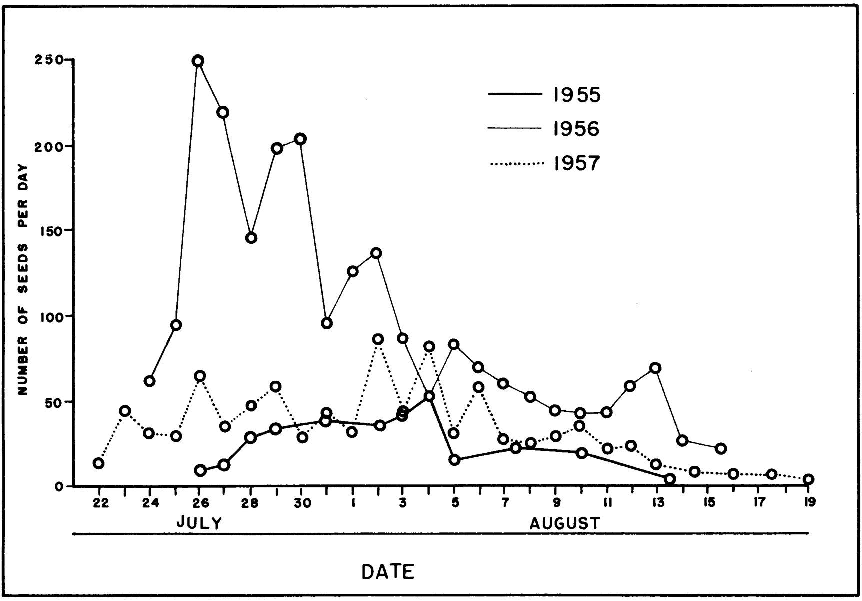

FIGURE 29.—Number of dwarfmistletoe seeds found per day on 30 seed traps in 1955, 1956, and 1957. Fort Valley Experimental Forest, Ariz.

test covered nearly the entire dispersal period. Most of the seeds were expelled during the last week in July and the first 2 weeks in August. Peak discharge dates were August 4, 1955; July 26, 1956; and August 2, 1957.

Relationship Between Seed Dispersal Period and Climatic Conditions

The seed dispersal period of *Arceuthobium vaginatum* f. *cryptopodum* coincides approximately with the summer rainy season. Other species of *Arceuthobium* in the Southwest and in the rest of the country mature in the autumn.

In general, the summer rainy season in the Southwest begins about the middle of July and lasts until about the end of August, although the duration and intensity of the rains vary. At the Fort Valley Experimental Forest, Ariz., July and August are the wettest months. Each average more than 3 inches of precipitation; the early summer months (May and June) are typically much drier and average about three-fourths of an inch of rain (Pearson 1950, p. 17). Information is given in the appendix on the weather at Fort Valley during July, August, and September for the years when the seed dispersal study was conducted. Measurable rain fell on nearly 60 percent of the days during the seed dispersal period from July 16 to August 15. Rainfall was considerably less before and after this period. The relative humidity was approximately 100 percent for an average of about 11 hours per day during the seed dispersal period. From July 16 to August 15, the mean maximum temperature was 77°, and the mean minimum was 45°, for an average difference of 32°. The difference between the daily extremes was greater before and after the seed dispersal period.

Dips in the 1956 seed dispersal curve (fig. 29) on July 27 and 31 were concurrent with cloudy, rainless days. The other days were either sunny or rainy. This suggests that there might be a relationship between daily weather and number of seeds discharged. However, statistical tests revealed no significant differences.

RATE OF SPREAD OF DWARFMISTLETOE THROUGH PONDEROSA PINE STANDS

Some reports have overestimated the rate of spread of dwarfmistletoes. Hedgcock (1913) estimated that *Arceuthobium americanum* in lodgepole pine in Colorado progressed at a rate of 6 to 12 feet annually. Parker (1942) reported an infection center in lodgepole pine in Alberta that covered 1.57 acres in 60 to 70 years, indicating a rate of spread of about 2 feet a year. Recent measurements made in 33 lodgepole pine stands in Colorado and Wyoming (Hawksworth 1958) showed that the rate of spread was 1 to 1.5 feet per year. Comparable studies have not been previously conducted with *A. vaginatum* f. *cryptopodum* in ponderosa pine, but Pearson (1950, p. 163) uses 50 feet per decade in discussing this species. However, this rate of spread was not based on actual measurements and was merely used as an example. The results reported here indicate that the rate of spread is less than one-half that mentioned by Pearson.

FACTORS INFLUENCING RATE OF SPREAD

Locally, dwarfmistletoe is spread primarily by the explosive fruits that eject the seeds for several feet. (Distance of seed flight was given in an earlier section, p. 52.) In long-distance spread, e.g., in the establishment of new infection centers at points beyond the effective range of the explosive fruits, birds are presumed to be instrumental. Wind does not seem to be important in the dissemination of this species in the Southwest. Only local spread is dealt with here.

The type of stand as a marked influence on the rate of spread of dwarfmistletoe. Spread is most rapid from overstory trees to an understory, while spread through even-aged stands is comparatively slow. In general, dwarfmistletoe progresses faster through open stands than through dense ones. However, where the distance between trees approximates the distance of seed flight, spread is limited.

The early stages of spread from overstory to understory are relatively complicated. Initially, all the infections in the young stand are first-generation infections; that is, they develop directly from seeds produced in adjacent overstory trees. Then there is a transition period when infections in the young stand begin to produce seeds that further infect the stand (second-generation infection). Subsequently, the infection progresses in the young stand outward beyond the range of the seeds produced in the overstory stand. This spread through even-aged stands, beyond the limits of seeds from an overstory source, is here termed lateral spread.

In this report, periodic rates of spread are given only for stands in which lateral spread had begun (or roughly those which had been infected for at least 20 years). The spread of infection from an overstory directly to an understory (first-generation infection) is not amenable to calculation on a periodic basis. For example, if an infection in a 10-year stand is found 50 feet away from the source overstory tree, it is misleading to say the parasite traveled 5 feet a year, because the seed probably traveled the distance at one time and not periodically.

METHODS

To measure the rate of spread of *Arceuthobium vaginatum* f. *cryptopodum* through ponderosa pine stands, only areas were used where all infection could be definitely traced to a single source tree or group. The distance the parasite had progressed from source trees was measured, and the length of time the stand had been subject to the parasite was determined. If the parasite was present in overstory trees before the adjacent reproduction became established, the age of the young stand was taken as the time of exposure to the parasite. However, in even-aged stands the length of time the dwarfmistletoe had been present was determined by dissecting and determining the age of a number of the oldest infections present in the area.

Care was taken in the selection of the plots to exclude those where the source of infection was doubtful. Suitable areas were relatively rare, since in most infected stands the disease is rather general as a result of the overlapping of numerous infection centers. These stands cannot be used for measurement of spread, for the source of individual infections cannot be determined. Because of the scarcity of suitable areas, it was not possible to set up the study on a statistical basis. Plots were established intermittently over several field seasons whenever suitable areas were found in connection with dwarfmistletoe surveys or other research work. For this reason, it was usually not possible to obtain detailed information on amount of infection in the young stands.

Measurements of distance of infection were made from the center of the bole of the source tree or trees to the bole of the farthest infected tree in the young stand. In most plots the spread in one direction was measured. If time was available, maximum distance of spread in two or more directions was determined, and the average distance was used for the plot.

Age of the young stand was determined by either increment cores of at least three dominant or codominant trees or ring counts on three stumps. If the ages of the first three trees varied by 5 years or more, three additional trees were measured.

Two density classes for young stands were used: "open" stands were defined as those where the crown canopy had not closed, and closed-canopied stands were classed as "dense." As the two classes graded into each other, there were some intermediate stands but, as will be shown, there were statistically significant differences in the rate of spread in the two density classes.

RESULTS

Two general types of spread were measured: (1) spread from overstory stands to adjacent young stands, and (2) lateral spread through even-aged stands.

Spread From Overstory to Young Stands

In discussions of spread of dwarfmistletoe from overstory stands to young stands, it should be kept in mind that two types are involved: (1) the first-generation infections resulting from seed produced in the overstory, and (2) subsequent infections that develop in the young stand from seed produced by first-generation infections, which in turn carry the limits of infection beyond the range of seeds produced in the overstory. Because information on distance of first-generation infection was already available (Gill 1954; Gill and Hawksworth 1954), the primary emphasis in these studies was on subsequent spread of the parasite in young stands after it had become well established.

Spread Directly From the Overstory

Gill and Hawskworth (1954) measured the distance of nearly 2,000 infected seedlings from the source overstory trees. Since nearly all infections were established before the overstory trees were removed, it was believed that these were nearly all first-generation infections. It was found that 81 percent of the infected seedlings were within 35 feet of the bole of the nearest infected overstory trees; 95 percent were within 45 feet; and 99 percent within 55 feet.

Information on first-generation infection was obtained in the Lincoln National Forest in southern New Mexico. Measurements were made in a 60-year-old pole stand that had been burned about 12 years before the study. The fire was so severe that only isolated trees and groups survived. The area was replanted shortly after the burn and, in addition, good natural reproduction occurred. Since most of the trees that survived were heavily infected, the area represented a unique opportunity to measure the distance of spread from these trees to the 10-year-old reproduction. The results show that the greatest distance between the infected young trees and the overstory averaged 42 feet, with a maximum of 86 feet:

Plot number	*Measurement basis (number)*	*Maximum distance of infection*	
		Average (feet)	*Range (feet)*
3	5	20	9–34
4	7	59	33–86
5	4	39	26–53
6	2	44	38–50
Total average	18	[1] 42	-----

[1] Standard error, ±5 feet.

Subsequent Spread in the Young Stand

The distance dwarfmistletoe had spread from overstory stands into 33 young stands is given in figure 30. Basic data for these plots is given in the appendix. Figure 31 is a crown map of one of the study areas. Information was obtained in 21 open stands from 23 to 49 years old and in 12 dense stands from 30 to 51 years old. Because these stands had been infected long enough for lateral spread to have begun, annual rates of spread were calculated for them. It was not possible to determine whether an individual infection had resulted from seed produced in the overstory or from seed produced in the young stand; hence, distance of infection in figure 30 represents spread directly from the overstory plus lateral spread. The fact that these data could be accurately represented by sloping lines indicates that lateral spread had begun.

The average rate of spread of the parasite was 1.7±0.1 feet a year into open stands and 1.2±0.1 feet a year into dense ones. These averages are not precise; the actual rate of spread decreases with time, for the distance infected directly from the overstory is a progressively smaller proportion of the total infected distance. However, the averages are useful in comparing the rate of spread in

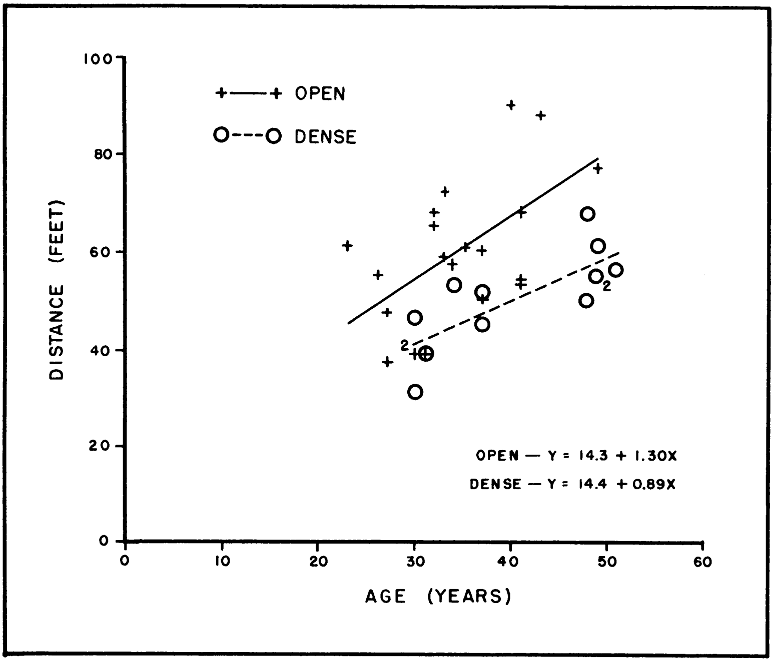

FIGURE 30.—Maximum distance of spread of dwarfmistletoe from overstory stands into adjacent young stands. Spread directly from the overstory plus lateral spread. Based on 21 open and 12 dense stands in Arizona and New Mexico.

stands of the same age. An example of the rate of spread in relation to time is shown below for open stands (fig. 30):

Average age (years)	*Maximum distance of infection (feet)*	*Average annual spread (feet)*
25	47	1. 9
50	80	1. 6

The presumed average maximum distances of infection into stands younger than those measured are shown by dotted lines in figure 32. The horizontal parts of the dotted lines represent the assumed effective range of seeds from infections in the overstory. The two curves for each species of mistletoe converge at a point somewhere under 20 years, since here infection is directly from seeds dropping into the stand from the overstory and density of the young stand would have little effect on the distance of such infection. Also, all very young stands would be "open" by the definition used, since there is no crown

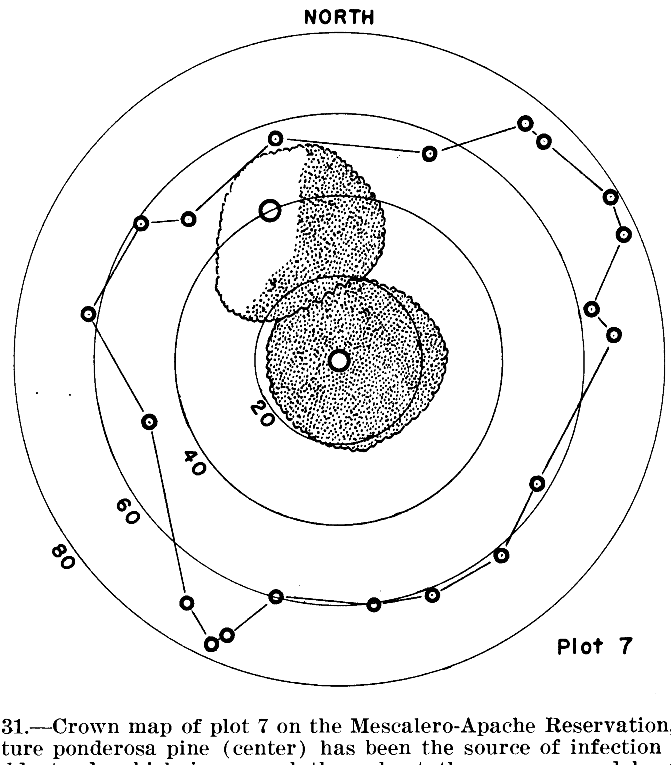

FIGURE 31.—Crown map of plot 7 on the Mescalero-Apache Reservation, N. Mex. A mature ponderosa pine (center) has been the source of infection for a 32-year-old stand, which is general throughout the area covered by the map. Crown projections of the two mature trees in the area are shown; the stippling indicates the proportion of the crown infected. Concentric 20-foot circles show the distance of spread of the parasite into the young stand. Only the infected young trees that were farthest from the source tree are shown (small circles). Average maximum distance of infection to the west, south, and east was 65 feet. Spread to the north and northwest was somewhat less, because the other mature trees screened the reproduction in these directions.

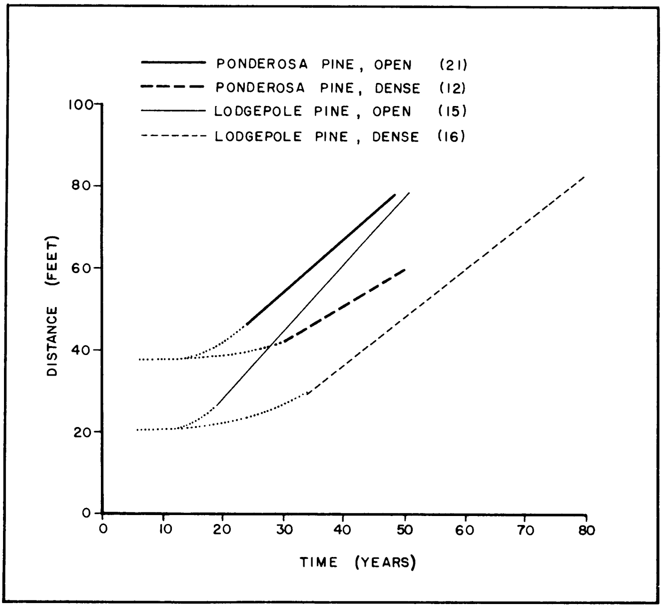

FIGURE 32.—Comparison of rate of spread of ponderosa pine and lodgepole pine dwarfmistletoes in stands of two densities. Spread from overstory stands to young stands and lateral spread in the young stand. Plot basis for each curve is shown in parentheses. The dotted parts of the curves are extrapolations for stands younger than those measured. Horizontal parts of the dotted lines indicate estimated effective range of seeds from the overstory. Spread beyond the horizontal dotted lines (or beyond about 20 feet for lodgepole pine dwarfmistletoe and about 40 feet for the species on ponderosa pine) is lateral spread.

closure in such stands. It is only after lateral spread in the young stands has begun that differences due to stand density are apparent.

In stands about 20 years old (fig. 32), practically all infection was attributable to seed produced in the overstory, but in 50-year-old stands lateral spread accounted for about half of the spread in open stands (the farthest 40 feet of the total 80-foot distance) and one-third of the total in dense stands (the farthest 20 feet of the 60-foot distance).

Rate of spread for *Arceuthobium vaginatum* f. *cryptopodum* in ponderosa pine is compared in figure 32 with that for *A. americanum* on lodgepole pine as reported by Hawksworth (1958). *A. vaginatum* spread slightly faster than *A. americanum* in both open and dense stands. Average rate of spread for all lodgepole pine plots was 1.2 feet per year, while that for ponderosa pine was about 1.5 feet per year. Most of the difference is due to the greater distance of seed flight from the overstory for ponderosa pine dwarfmistletoe, since the slopes of the lines are steeper for lodgepole pine dwarfmistletoe, indicating a faster rate of lateral spread for this species.

The hypothetical relationship between stand density and rate of spread of dwarfmistletoe is presented in figure 33. Spread is relatively slow through dense stands, but increases as density decreases up to the point where the trees are so far apart that transfer of the para-

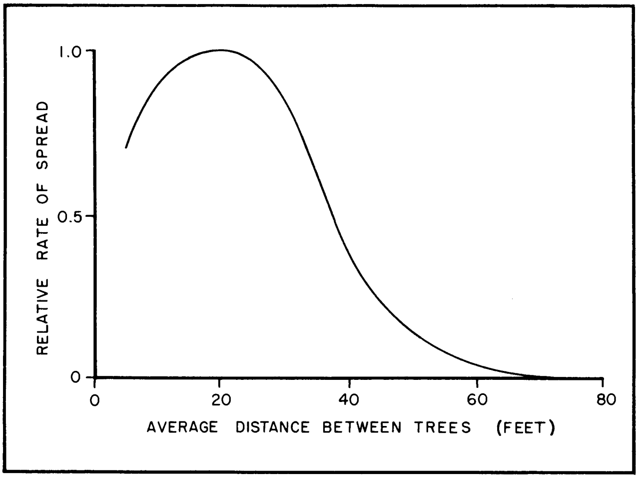

FIGURE 33.—Hypothetical relationship between stand density and rate of spread of ponderosa pine dwarfmistletoe. The curve represents stands about 30 to 40 years old. It would be shifted to the left for younger stands and to the right for older ones.

site from one tree to another becomes more difficult. The rate of spread then decreases with decreasing stand density and reaches zero when the distance between the trees exceeds the distance of horizontal seed flight.

Because most of the plots were on relatively level ground, little information was obtained on the relationship between the rate of spread of this mistletoe and steepness of slopes. Weir (1923) and Kimmey (1957, p. 10) state that dwarfmistletoes spread faster downhill than uphill. However, Hawksworth (1958) found no relationship between degree of slope and rate of spread of *Arceuthobium americanum* in lodgepole pine.

The results indicate no significant relationship between compass direction and distance of spread. This is in agreement with previous work on *Arceuthobium vaginatum* f. *cryptopodum* (Gill and Hawksworth 1954), and it provides further evidence that prevailing winds are not important in the dissemination of this species.

Lateral Spread Through Even-Aged Stands

Occasionally, it was possible to measure lateral spread exclusively without the complication of infection from an overstory, such as in even-aged stands infected several years after they were established. Measurements of lateral spread were obtained in six centers. Usually, the parasite had been present for such a short time that it was possible to identify the tree that became infected first and from which, presumably, all further infection in the center developed. It is assumed that birds are responsible for the establishment of new infection centers in healthy stands, although nothing definite is known.

Since in even-aged stands there is no initial boost due to seed flight from an overstory, it would be expected that the rate of spread of the parasite would be somewhat less than that for spread from overstory stands into reproduction. Dwarfmistletoe had been established for an average of 44 years in the six centers. The infected areas had an average radius of 40 feet, thus indicating an annual spread of 0.9 foot. Lateral rate of spread is shown in figure 34, and the basic data for the six study areas are tabulated in the appendix. A stem map of one of the study plots is shown in figure 35. As previously mentioned, in spread from an overstory to a young stand, the annual rate of spread decreases with time, for the distance infected directly from the overstory is a progressively smaller proportion of the total infected distance. The annual rate of spread in such stands decreases gradually until it approaches that for exclusively lateral spread or about 1 foot a year.

Area Covered by Infection Centers of Different Ages

As pointed out by Pearson (1950, p. 163), the area covered by an infection center increases as the square of the radial spread. This is important, because relatively small differences in radial rate of spread result in proportionally great area differences. The area covered by infection centers in the three types of stands up to 80 years old is shown in figure 36. Although the radial spread averages only about one-third greater from an overstory to open than to dense stands, the area of infection centers is nearly twice as great in open as in dense stands infected for the same length of time.

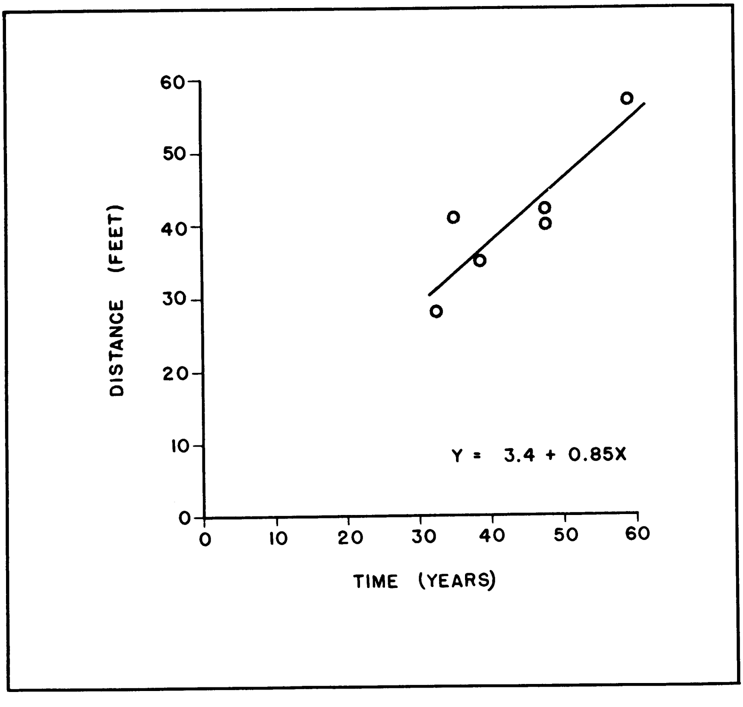

FIGURE 34.—Rate of spread of dwarfmistletoe through six even-aged ponderosa pine stands.

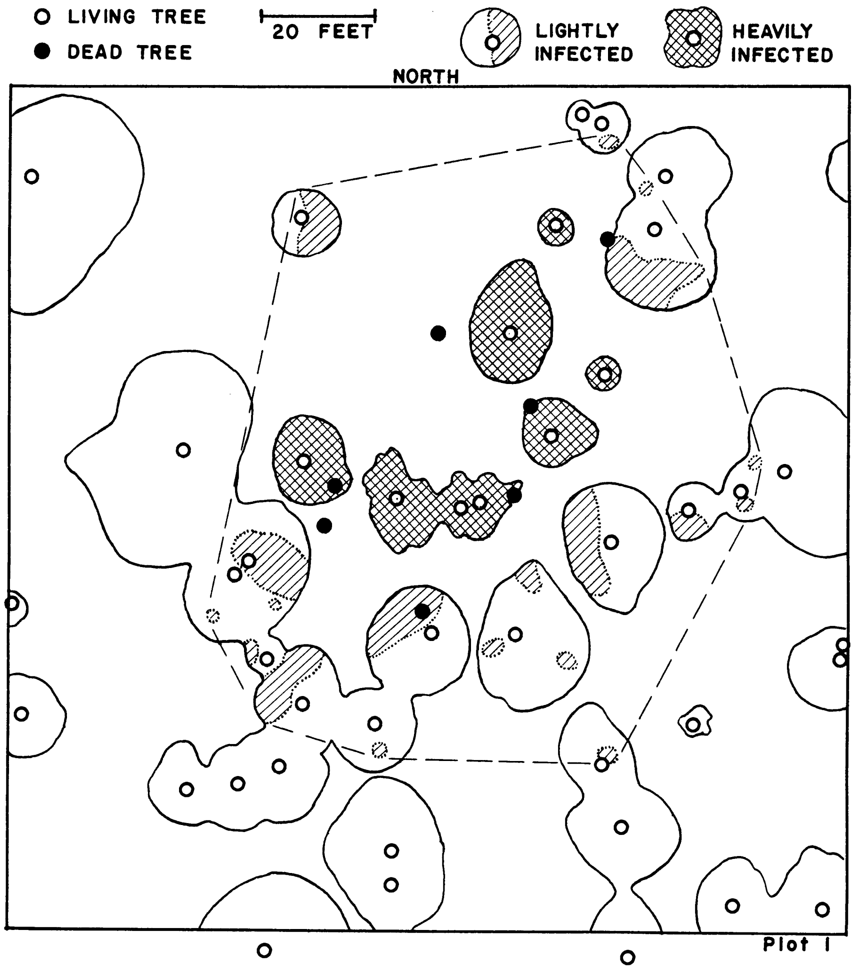

FIGURE 35.—A stem and crown projection map of spread plot 1 showing an infection center in an even-aged, 100-year-old stand at the Grand Canyon National Park, Ariz. The parasite had been established here for about 60 years. The infected area (within the dashed line) amounts to approximately one-fourth acre. Healthy trees and those lightly infected averaged 13.6 inches d.b.h.; heavily infected trees and those recently killed by dwarfmistletoe averaged 7.9 inches d.b.h.

EFFECTS OF DWARFMISTLETOE ON THE GROWTH OF PONDEROSA PINE

It is well known that heavy infections of *Arceuthobium vaginatum* f. *cryptopodum* markedly reduce the growth rate of ponderosa pine (Korstian and Long 1922; Sperry 1934; Pearson and Wadsworth 1941; Pearson 1950), but there is little information on the extent of this reduction in extensive host populations.

The primary objectives of this study were to determine the relative effects of different degrees of infection on recent radial increment,

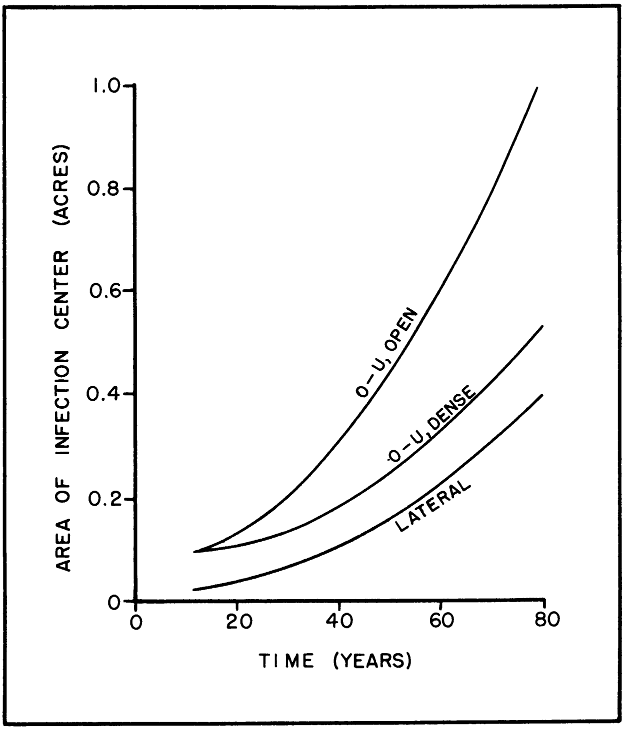

FIGURE 36.—Area of infection centers in three types of ponderosa pine stands. Overstory to understory spread is indicated by "O–U," and "Lateral" represents lateral spread in even-aged stands.

total diameter, height growth, and volume of ponderosa pine. Such information is needed to obtain estimates of growth losses on a regional basis. A survey recently completed has provided estimates of the number of trees in various infection classes (Andrews and Daniels 1960). The Mescalero-Apache Reservation in southern New Mexico was chosen for the measurement, although data must be obtained from other localities before the results can be considered as representative of the region. Another objective of the investigation was to compare the reduction in growth rate in this southern New Mexico locality with that reported in northern Arizona by Korstian and Long (1922).

Review of Previous Work

Weir (1916, p. 2) measured the effects of dwarfmistletoe on the growth of several conifers in the Northwest, including ponderosa pine affected by *Arceuthobium campylopodum* f. *campylopodum*. Measurements of 50 heavily infected and 50 uninfected 100-year-old trees showed that radial growth for the 40-year period before the study was 71 percent lower in the infected trees. Effects of dwarfmistletoe on total height and diameter were less pronounced, because the infected trees were 36 percent shorter and 18 percent smaller in diameter than the uninfected trees.

A comprehensive report of the effects of *Arceuthobium vaginatum* f. *cryptopodum* on ponderosa pine in northern Arizona was published by Korstian and Long (1922). This study was based on measurements of 91 standing trees and on stem analyses of 107 felled trees. The authors did not summarize their results quantitatively but concluded dwarfmistletoe causes a marked decrease in growth rate that continues until the parasite ultimately kills its host. The decrease in growth rate varied directly with degree of infection, ranging from little or no reduction in lightly infected trees to a very marked falling off in the current increment of heavily infected trees. Radial increment for a 5-year period in heavily infected trees was 12 to 14 percent of that of uninfected trees. Comparable figures for gross cubic-foot increment were 15 to 31 percent. Diameter and total height of heavily infected trees were about one-third less than those of uninfected trees.

A small-scale study on the effects of this species of dwarfmistletoe on ponderosa pine in Colorado was reported by Sperry (1934). A camparison was made of radial increment between five infected and five uninfected 75-year-old trees growing in a small area. At the time of measurement, the infected trees were growing at a rate of 60 percent of that of the uninfected trees, although initially the infected trees were growing faster than the healthy ones.

Pearson (1950, p. 164) and Pearson and Wadsworth (1941) note the effects of dwarfmistletoe on board-foot increment over a 30-year period in a ponderosa pine stand in northern Arizona. Uninfected trees produced an average increment during this period of 205 board feet, lightly and moderately infected trees averaged 213 board feet, and heavily infected trees produced 133 board feet. The slightly higher increment in lightly and moderately infected trees was not regarded as significant, but the heavily infected trees produced 35 percent less than the uninfected trees.

METHODS

Information was obtained on uninfected trees and those with various degrees of infection growing in the same area The sample areas were selected to include a relatively uniform site, and their size ranged from 2 to 5 acres in poles and from 10 to 15 acres in merchantable-sized trees Emphasis was on dominant trees, although a limited sample was made of the lower crown classes. The diameter, total height for poles or log height for merchantable trees, vigor rating, crown class, and degree of infection were recorded for each tree. The cubic-foot volume of poles and the board-foot volume of merchantable trees were later determined from regional volume tables. An increment boring was taken on the north side of each tree at breast height. Each core was assigned a code number and measurements of radial growth were made. Details on the factors recorded for each tree follow:

1. **Diameter.** The diameter at breast height was measured to the nearest 0.1 inch with a diameter tape.

2. **Height.** Total height of pole-sized trees was determined to the nearest foot by placing a 40-foot pole, which was marked at 5-foot intervals, next to the tree and estimating the height from a distance of at least 1 chain. Log height of merchantable-sized trees was estimated to the closest one-half log.

3. **Vigor.** The vigor of each tree was classed as good, fair, or poor on the basis of needle color and foliage density of the upper one-third of the crown. Trees with normal colored needles and dense crowns were classed as "good", and those with normal colored needles but with less dense crowns were classed as "fair". Trees classed as "poor" had off-colored foliage or very thin crowns.

4. **Crown class.** Four crown classes were used—dominant, co-dominant, intermediate, and suppressed.

5. **Mistletoe rating.** A 6-class mistletoe rating system described by Hawksworth and Lusher (1956) was used. The live crown is divided into thirds, and each third is rated as: 0, no mistletoe; 1, light mistletoe (less than one-half of branches infected); and 2, heavy mistletoe (more than one-half of branches infected). The ratings of each third are added to obtain a total for the tree. For example, a tree heavily infected in the lower one-third of the crown, lightly infected in the middle one-third, and not infected in the upper third would be class 3. A tree heavily infected in each third would be class 6. Initial dwarfmistletoe infection usually takes place near the base of the tree crown and spreads upward, so in a class-3 tree usually only the lower half of the crown is infected; in a class-4 tree, the lower two-thirds, etc. This system is simple to use, and ratings of the same trees by different observers are comparable. It was adopted rather than the 3-class system that was used by Korstian and Long (1922, p. 4–5), because more detail was desired. It indicates the abundance of the parasite in various parts of the crown rather than its mere presence. As will be shown, the 6-class system can also be used to indicate the degree of growth reduction caused by dwarfmistletoe. It cannot, however, be used as a measure of infectiveness, for this is frequently independent of the amount of mistletoe in a tree.

An effort was made to obtain increment cores that included the pith, but no reborings were made if this was not accomplished. Total age of the trees at breast height was available from about one-quarter of the cores. This was sufficient for averages in these even-aged stands.

Before the cores were measured, several from uninfected trees in each area were analyzed to determine characteristic patterns of wide and narrow rings so that definite years could be assigned to the rings on each core. This was essential, because growth of some heavily infected trees was so slow that the most recent rings could not be distinguished even with the use of a binocular microscope. Measurements of growth during the last 5 years prior to the date of the sample were made for all cores; also, growth by 5-year periods for poles and by 10-year periods for merchantable trees were recorded. These measurements were made with a ruler divided into sixtieths of an inch, and calculations based on them were later converted to hundredths of an inch for presentation.

Results

A total of 1,603 trees in 2 age classes was measured (table 6). At breast height, these age classes averaged 43 years for poles and 129 years for merchantable timber. Total age was estimated at 55 and 140 years, respectively. About one-third of the trees were measured in the fall of 1952 and the remainder in the fall of 1955.

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TABLE 6.—*Summary of the five areas established to study effects of dwarfmistletoe on the growth of ponderosa pine, Mescalero-Apache Reservation, N. Mex.*

Stand type, area, and logging unit	Year of study	Average age at breast height	Approximate size of study area	Tree basis
		Years	*Acres*	*Number*
Pole stands:				
B, Whitetail	1952	38	2	266
D, Snow	1955	46	5	408
E, Whitetail	1955	45	2	225
Total			9	899
Merchantable stands:				
A, North Tularosa	1952 & 1955	125	15	406
C, Carrizo	1955	134	10	298
Total			25	704

One of the pole stands (area D) was thinned between 1930 and 1935, or when the trees were between 30 and 35 years old. There are no records of the thinning, but presumably visibly infected trees were cut; this is known to have been done in nearby thinnings made about the same time. The other two pole stands had received no cultural treatment. Area A was lightly logged about 25 years prior to the study, and area C was in a virgin stand.

Effects on Radial Increment

The effects of dwarfmistletoe on recent radial growth (last 5 years) and periodic growth by 5- or 10-year periods are discussed separately.

Recent Growth

Average radial growth during the 5-year period before measurement for all trees in the two age classes is given in figures 37 and 38. Data for all areas in each age class were combined, since there were no significant differences in recent growth. This was true even for area D, which was thinned about 20 years previously. Also, different years growth were represented by the last 5 years, because some borings were made in 1952 and others in 1955; however, these were grouped because differences were slight. In the 55-year-old pole stands, significant growth reduction occurred only in trees of infection classes 5 and 6; radial increment during the 5 years before measurement was 19 and 35 percent, respectively, less than that of uninfected and lightly infected (class 0, 1, and 2) trees. Photographs of a healthy tree and two infected with dwarfmistletoe in area D are shown in figure 39. In 140-year-old dominants, growth during the past 5 years for classes 4, 5, and 6 was reduced by 14, 26, and 52 percent, respectively, in comparison with uninfected and lightly infected trees. However, only the reduction in classes 5 and 6 was statistically significant.

The results for codominant and intermediate trees (figs. 37 and 38) have been grouped, because there were no significant differences between them. Although the basis for these lower dominance classes is relatively weak, the results suggest that the effects of dwarfmistletoe on them is less pronounced than on dominant trees.

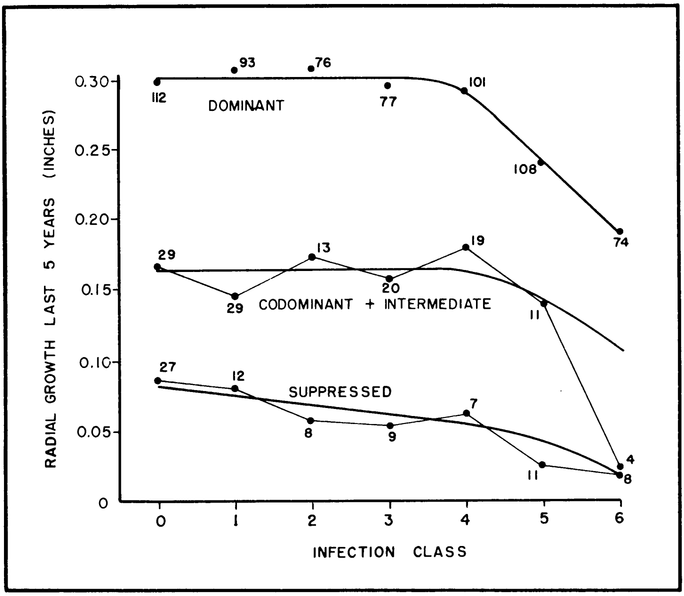

FIGURE 37.—Recent radial increment (last 5 years) in relation to degree of infection and crown class in 55-year-old pole stands. Basis: 848 trees. Mescalero-Apache Reservation, N. Mex.

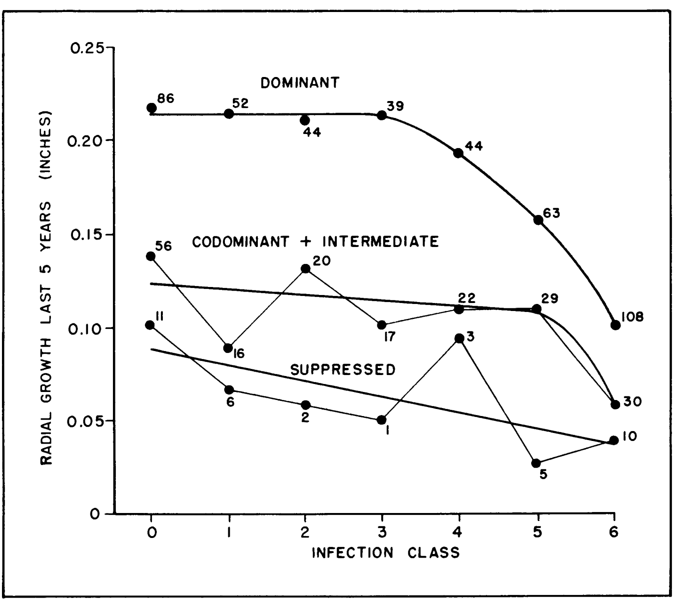

FIGURE 38.—Recent radial increment (last 5 years) in relation to degree of infection and crown class in 140-year-old merchantable stands. Basis: 664 trees. Mescalero-Apache Reservation, N. Mex.

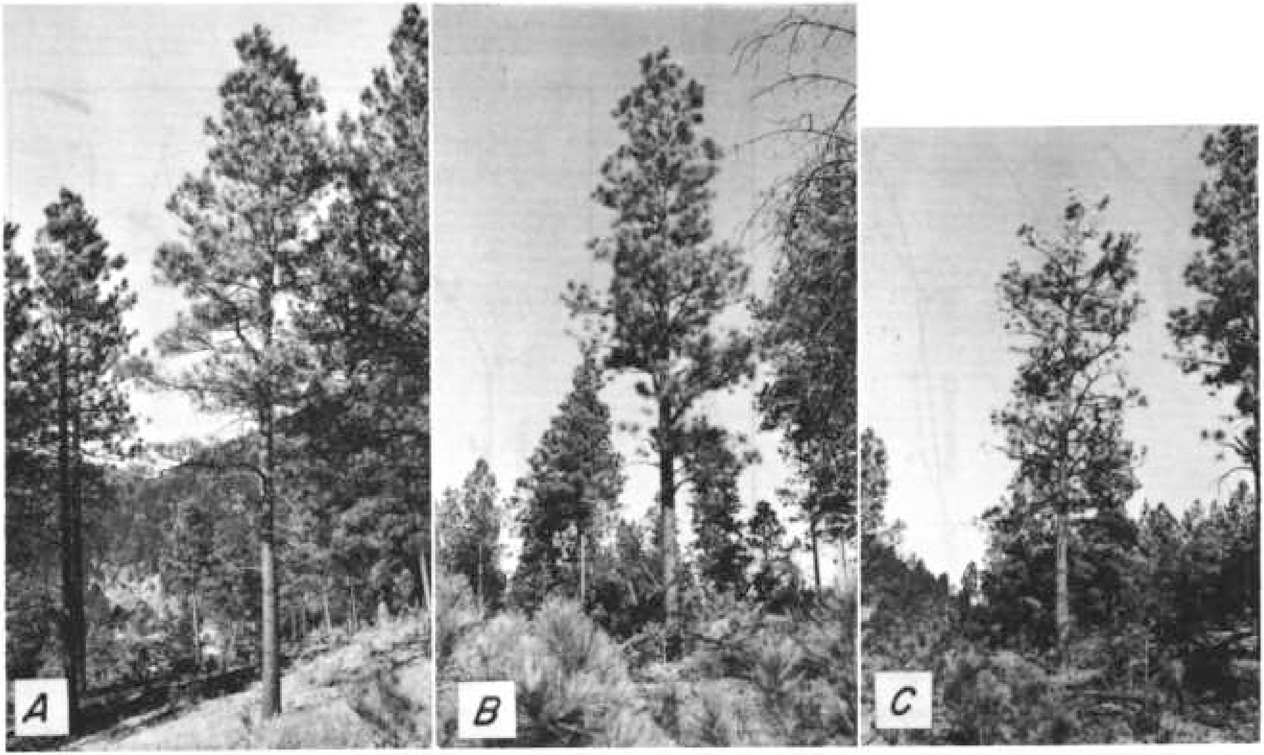

FIGURE 39.—Examples of trees from growth study area D in a 55-year-old pole stand on the Mescalero-Apache Reservation, N. Mex. *A*, An uninfected tree (49.0 feet high and 11.9 inches d.b.h.; *B*, a moderately infected (Class 3) tree (43.0 feet high and 10.8 inches d.b.h.) ; *C*, a heavily infected (Class 6) tree (33.5 feet high and 9.3 inches d.b.h.). Note the poor vigor of this tree.

Periodic Growth

The radial growth in dominant poles by 5-year periods is given in figures 40 and 41. In both these figures all measurements for uninfected and infected trees of classes 1 through 4 were combined into one group, since there were no marked differences between them. The increased growth rate in area D between 1935 and 1945 was a result of the thinning in this stand between 1930 and 1935. In area B, which had received no cultural treatment, growth of heavily infected trees (classes 5 and 6) had only recently begun to fall below that of the uninfected and lightly infected trees. In area D, growth in all dominant trees up until about 1930 was very similar (fig. 41). The trees of class 5 at the time of the study had lower than average growth for the last 5 to 10 years; and class 6 trees, for the last 10 to 15 years. Periodic growth rate of the seven trees killed by dwarfmistletoe was reduced for 15 to 20 years prior to their death.

Ten-year periodic growth for dominant trees of various infection classes in the 140-year-old stand in area A is shown in figure 42. Uninfected trees (class 0) and lightly infected trees (classes 1 through 3) were grouped because differences were slight. There was a uniform reduction with increasing degree of infection only in the last 10 years. Variables other than the amount of dwarfmistletoe probably account for the discrepancies. Because of the size of the trees, the sample was spread over a larger area (15 acres), so variations in site were probably greater than in the pole stands.

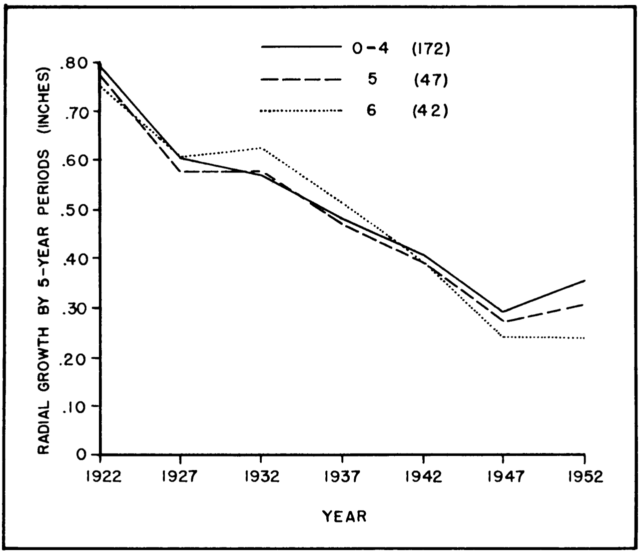

FIGURE 40.—Radial growth, by 5-year periods, of dominant poles that had various degrees of infection (area B). Infection class and tree basis for each curve are shown in the legend. Basis: 261 trees; average age: 38 years at breast height. Mescalero-Apache Reservation, N. Mex.

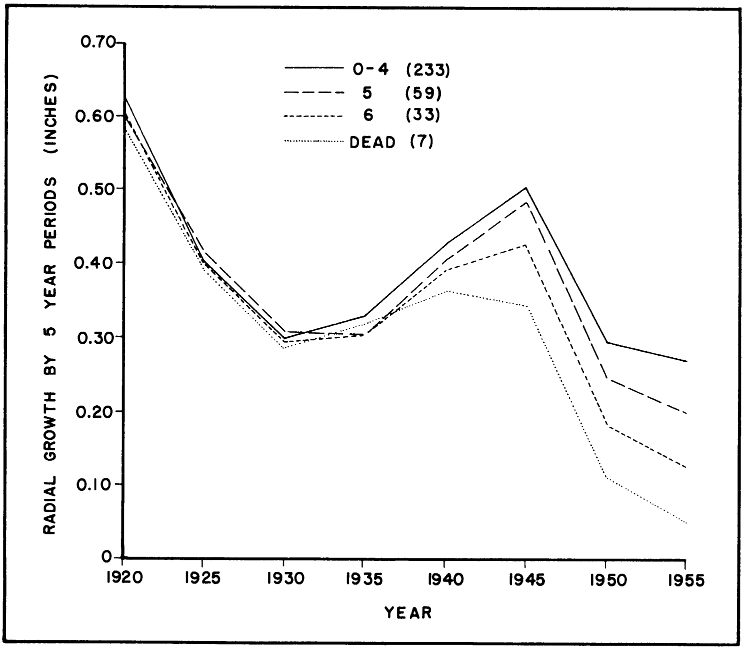

FIGURE 41.—Radial growth, by 5-year periods, of dominant poles that had various degrees of infection (area D). Infection class and tree basis for each curve are shown in the legend. Basis: 332 trees; average age: 46 years at breast height. Mescalero-Apache Reservation, N. Mex.

Effect of Brooms on Relative Growth Rate

When a tree becomes infected throughout the crown over a relatively short period of time, the formation of witches'-brooms may be delayed or completely inhibited. A comparison was made between radial growth of poles of the same infection class that had developed brooms and those that had not. The reduction of radial growth in broomy trees was considerably greater than in nonbroomy trees with the same proportion of the crown infected (table 7). Even for heavily infected trees (class 6), radial growth in those with nonbroomy infection was reduced only 14 percent compared with a reduction of 59 percent in trees with brooms. The difference between growth rate of trees with broomy and nonbroomy infections increased with degree of infection. For trees of infection class 6, radial growth of those with broomy infections was less than one-half that of the nonbroomy ones. The frequency of broomy trees increased with the degree of infection and ranged from 7 percent in trees of infection classes 1 through 3 to 68 percent in trees of class 6.

The relationship reported above for nonbroomy and broomy poles was essentially the same as that for dominant, class-6 trees in the 140-year-old merchantable stands.

Pearson and Wadsworth (1941) observed that in rare instances, "phenomenal" diameter growth occurred in infected trees prior to physical decline of the crown. One such tree was found in the

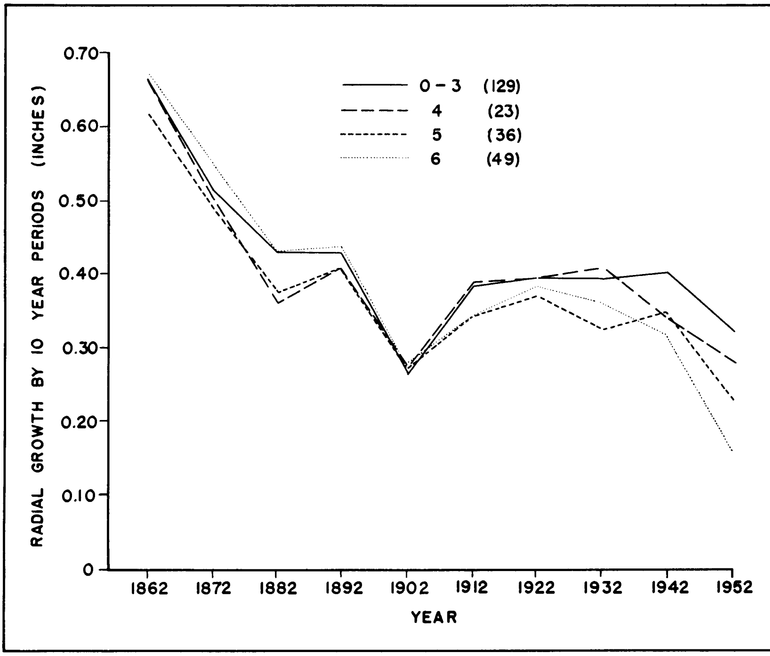

FIGURE 42.—Radial growth, by 10-year periods, of dominant, merchantable-sized trees (area A). The infection class and tree basis for each curve are shown in the legend. Basis: 237 trees; average age: 125 years at breast height. Mescalero-Apache Reservation, N. Mex.

present study. A heavily infected (class 6) dominant pole with nonbroomy infection showed a radial growth of 0.85 inch during the last 5 years. This compares with an average of 0.16 inch for all other class 6 dominants in this area and with 0.29 inch for uninfected dominants. The rapid recent growth rate of this tree was offset by slower than average growth prior to this time. Its total diameter was about the same as for other heavily infected trees. Because its rapid growth rate was not noticed at the time the core was taken, no search was made for factors that might account for it, such as release caused by the death of adjacent trees.

TABLE 7.—*Comparison of recent radial increment (last 5 years) of dominant poles with broomy and nonbroomy infection (area D)*

Infection class	Trees with nonbroomy infection		Trees with broomy infection		Frequency of broomy trees in each infection class
	Basis	Growth reduction [1]	Basis	Growth reduction [1]	
	Number	*Percent*	*Number*	*Percent*	*Percent*
1-3	110	0	8	0	7
4	38	0	21	7	36
5	23	7	36	45	61
6	11	14	23	59	68

[1] Growth during the last 5 years for trees of infection classes 1 through 3 was the same (0.29 inch) for both broom types.

Effects on Tree Size and Volume

The effects of dwarfmistletoe in dominant poles were most pronounced on cubic-foot volume, less on height, and the least on diameter (table 8). The height of poles in infection classes 4, 5, and 6 was significantly lower than that for the uninfected and lightly infected trees. Significant reductions in gross cubic-foot volume occurred in classes 5 and 6, but the reduction in total diameter was not significant in any infection class.

Average diameter, merchantable height, and gross board-foot volume for the 455 dominants in the 140-year-old stands are given in table 9. The relative effects of the parasite were similar to those in the pole stands—most pronounced on volume, intermediate on height, and least pronounced on diameter. The reduction in total diameter was not significant in either age class.

Effects on Host Vigor

The vigor of each tree was classed as good, fair, or poor on the basis of needle color and density of the foliage in the upper one-third of the crown. Because of the subjective nature of such a classification, no statistical analyses of the results were made, although a marked reduction in host vigor in heavily infected trees is unmistakable (fig. 43). The "poor" class was the least subjective, and trees in it had fading, off-color foliage or thin crowns. The proportion of poor-vigor trees was higher in the 55-year-old pole stands than in the older one, but both showed the highest proportion of poor vigor trees in infection class 6. In the pole stands, 61 percent of the class-6 trees were of poor vigor as compared with 24 percent in class 5 and an average of less than 2 percent for all other classes, including the uninfected trees. Twenty-eight percent of the class-6 trees in the 140-year-old stands were of poor vigor, as compared with 12 percent of the class-5 trees and an average of 3 percent of all other classes.

Comparison of Results With Previous Findings

In general, the results of this work agree with those of Korstian and Long (1922) in that the effects of light infection is negligible but that there is a marked reduction in recent increment in heavily infected

TABLE 8.—*Summary of average size of dominant poles*[1] *of various infection classes; combined data for areas B, D, and E, Mescalero-Apache Reservation, N. Mex.*

Infection class	Tree basis	Diameter at breast height	Total height	Gross volume
	Number	*Inches*	*Feet*	*Cubic feet*
0	114	10.7	48	13.0
1	99	10.0	44	10.5
2	82	10.1	45	11.0
3	78	10.3	43	10.8
4	103	10.3	[2] 42	10.5
5	110	9.9	[2] 40	[2] 9.0
6	76	9.5	[2] 36	[2] 7.6
Total	662			

[1] Average age, 55 years.
[2] Significant difference from grouped average of classes 0, 1, and 2.

TABLE 9.—*Summary of average size of dominant merchantable trees*[1] *of various infection classes; combined data for areas A and C, Mescalero-Apache Reservation, N. Mex.*

Infection class	Tree basis	Diameter at breast height	Merchantable height in 16-foot logs	Gross volume
	Number	*Inches*	*Number*	*Board feet*
0	90	21.4	4.0	450
1	53	21.5	3.8	430
2	45	22.9	3.9	520
3	43	21.6	3.9	490
4	49	21.8	3.6	430
5	68	20.8	3.7	[2] 390
6	107	20.3	[2] 3.3	[2] 300
Total	455			

[1] Average age, 140 years.
[2] Significant difference from grouped average of classes 0, 1, and 2.

trees. Direct comparison between the two studies is not possible, because different systems were used for classifying infected trees. Korstian and Long's results for lightly infected trees were very irregular; in some observations, the radial growth of those trees exceeded that of the uninfected trees, and in others it was one-third less. Variations in recent volume increment in lightly infected trees were even greater, ranging from 5 percent more to 74 percent less than for the uninfected trees. The marked reduction in growth rate of several of their lightly infected trees suggests that the uninfected trees were not really comparable to the infected ones, for in the present study there was no reduction in lightly infected trees. The irregular results may have resulted from the manner in which Korstian and Long selected their trees; these were apparently scattered over wide areas rather than in relatively small areas as in the present study.

In view of the large variation in growth rates of their lightly infected trees, Korstian and Long's (1922, p. 17) statement that light infections occasionally stimulate diameter growth of the tree cannot be regarded seriously. Gill (1935, p. 218) also considered that the slight increases noted were probably accounted for by experimental error. In the present study, there were no significant differences between lightly infected and uninfected trees in recent radial increment, total diameter, height, or volume.

WITCHES'-BROOMS ASSOCIATED WITH DWARFMISTLETOE

Witches'-brooms are growths of abnormal branching habit, commonly with unusually dense foliage, and are the most conspicuous symptom of trees infected with dwarfmistletoe. As pointed out by Kuijt (1955, p. 592), the ability of dwarfmistletoes to induce witches'-brooms makes them unusual among higher plants, although brooms are commonly produced by fungi, insects, and viruses. While brooms are not always associated with all species of *Arceuthobium*, they are characteristic of these parasites.

It is well known that different types of brooms are associated with various species of *Arceuthobium* on different hosts (Gill 1935, p. 212).

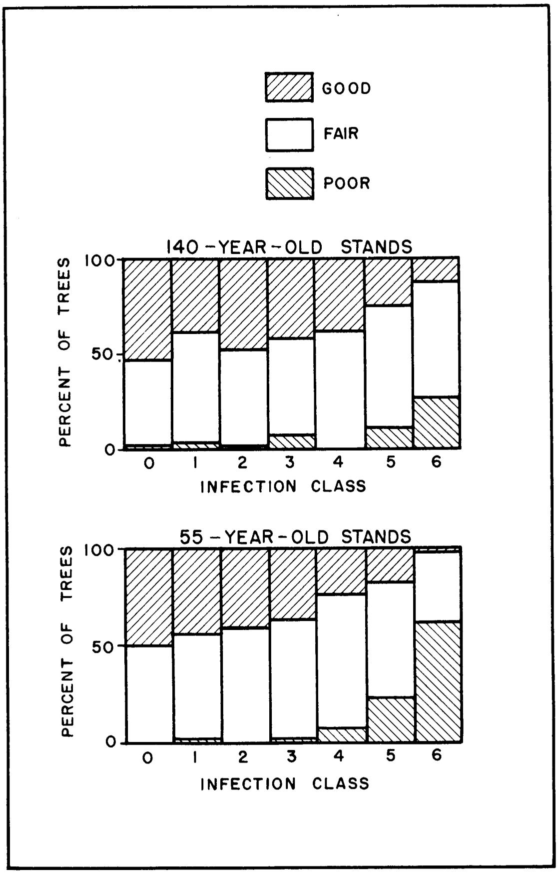

FIGURE 43.—Relationship between amount of infection and vigor of the host in two age classes. Basis: 899 trees in the young stand and 704 in the older one. Mescalero-Apache Reservation, N. Mex.

It seems to be less well known that a number of different types of brooms may be formed by the same parasite on a single host species. Three types are associated with *A. pusillum* on black spruce (Anderson and Kaufert 1959) and three are also reported here for *A. vaginatum* f. *cryptopodum* on ponderosa pine.

Types of Brooms on Ponderosa Pine

Before the types of brooms formed on ponderosa pine by dwarf-mistletoe are discussed, it should be noted that not all infections develop into brooms. Instances in which broom formation may be partially or completely inhibited are (1) infections on main stem, (2) infections on growth so old that no buds capable of growing into new branches are present, and (3) trees that become generally infected throughout the crown in a relatively short time (fig. 44).

The three general types of brooms associated with ponderosa pine infected by this parasite are as follows:

FIGURE 44.—Heavily infected (class 6) trees in which there has been relatively little broom formation, even though they have been infected for a long time. Infection is so general (every branch infected) that marked broom formation in any one branch is prevented. Grand Canyon National Park, Ariz.

1. *Typical brooms.* These are roughly spherical in outline, with a marked taper in the infected branches (fig. 45, *A*).
2. *Volunteer leader brooms.* These are brooms in which one or several branches assume a vertical habit (fig. 45, *B*).
3. *Weeping brooms.* The branches on these brooms show a definite drooping tendency (fig. 45, *C*).

Typical Brooms

Typical brooms are nearly isodiametric and may attain a diameter of 12 feet or more (fig. 46). The branches on this type of broom are characterized by their marked taper. This is by far the commonest type, and counts made in two 70-year-old stands on the Fort Valley Experimental Forest, Ariz., showed that these comprise about 85 percent of the brooms present (table 10).

Dissections of a few typical brooms were made to determine their growth rate. The brooming tendency of 10-year-old infections is

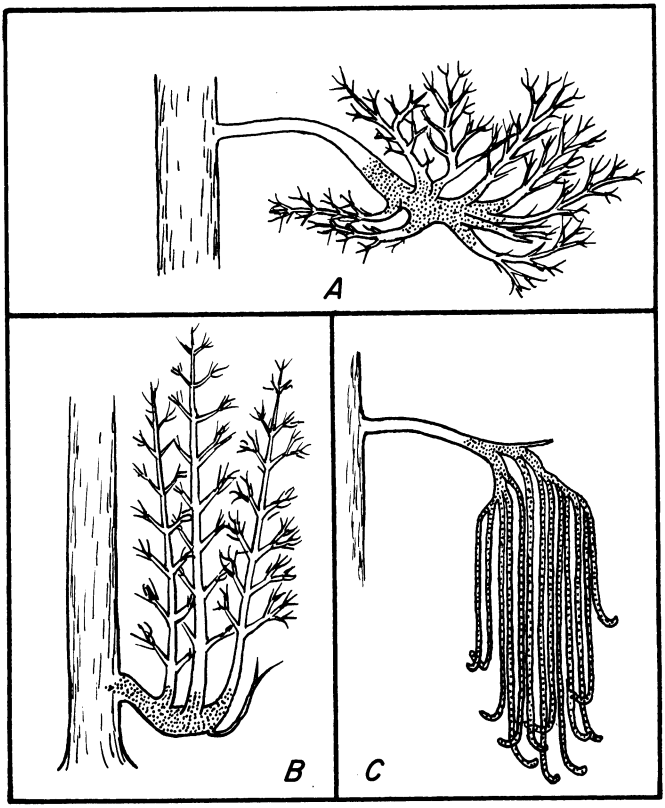

FIGURE 45.—Three types of brooms associated with dwarfmistletoe on ponderosa pine: *A*, Typical broom; *B*, volunteer leader broom; and *C*, weeping broom. The stippled areas indicate the areas actually invaded by the parasite.

scarcely distinguishable (fig. 47), but it is clearly evident in the two 18-year-old infections. Average diameter of brooms associated with the seven dissected infections is shown in figure 46. Vigor of the host also has a marked effect on growth rate of brooms; brooms on vigorous branches are larger than those of the same age on branches of lesser vigor. Twenty-year-old brooms averaged 3½ feet in diameter, while those 40 years old measured 5¾ feet (fig. 48). Between 10 and 40 years of age, the brooms increased in diameter at an average rate of 0.1 foot per year.

TABLE 10.—*Abundance of the three types of dwarfmistletoe brooms in two 70-year-old stands, Fort Valley Experimental Forest, Ariz.*

Broom type	Area A		Area B		Total	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*
Typical	565	87.8	219	78.5	784	84.9
Volunteer leader	76	11.7	54	19.4	130	14.1
Weeping	3	.5	6	2.1	9	1.0
Total	644	100.0	279	100.0	923	100.0

FIGURE 46.—Typical broom in infected ponderosa pine: *A*, Heavily infected tree on the Mescalero-Apache Reservation, N. Mex. The infection has lowered the vigor of the tree, and the tree has begun to die from the top. *B* and *C*, Broomed ponderosa pines killed by heavy dwarfmistletoe infection. Bryce Canyon National Park, Utah. *D*, A tree with a single broom about 12 feet in diameter in the lower crown. Grand Canyon National Park, Ariz.

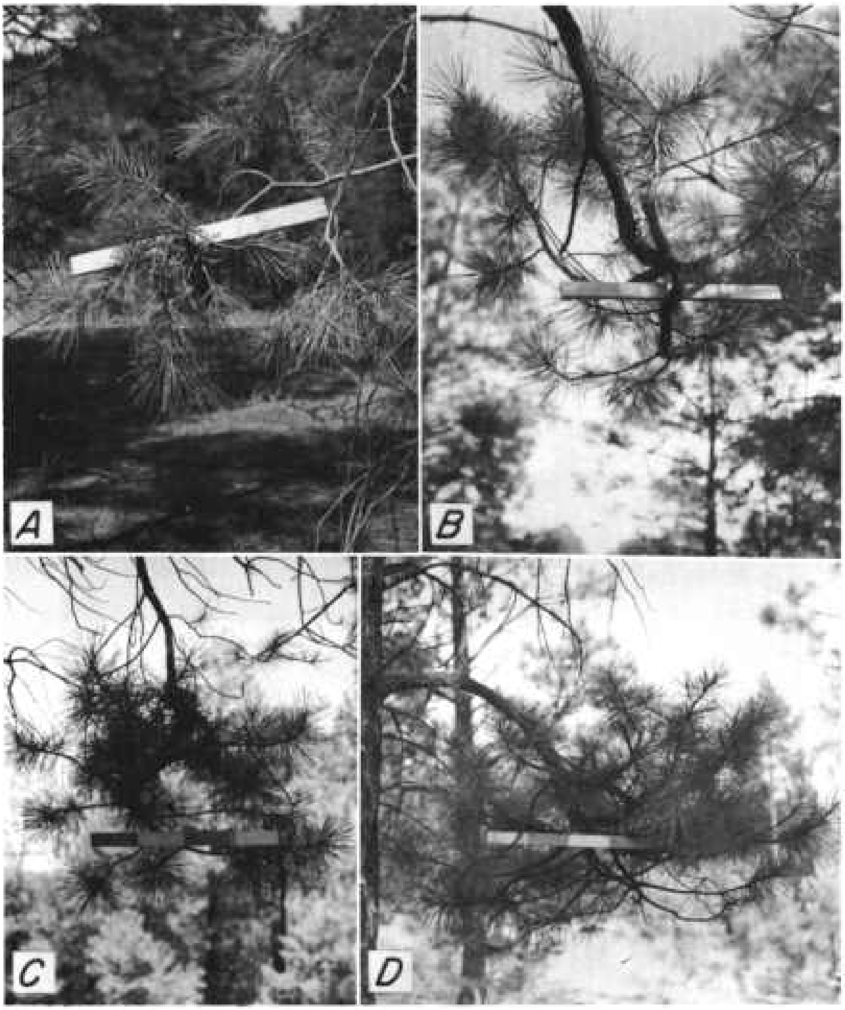

FIGURE 47.—Typical brooms of different ages on ponderosa pine. A 2-foot rule is shown in each photograph. *A*, An infection established for about 10 years. *B* and *C*, Infections established for about 18 years. *D*, A 36-year-old infection.

Volunteer Leader Brooms

Volunteer leader brooms are characterized by a marked vertical tendency of the branches (fig. 49). They occasionally rival the original leader in height and diameter (fig. 49, *B* and *C*). Dissections of only two volunteer leader brooms were made. Their height growth was four times the average radial growth of the seven typical brooms measured. These brooms are similar to those described by Anderson and Kaufert (1959) as "leader" brooms on black spruce infected by *Arceuthobium pusillum*. The name "volunteer leader" is used here instead of "leader" for these brooms; the latter name implies that infection takes place on the main stem, but this is not always true.

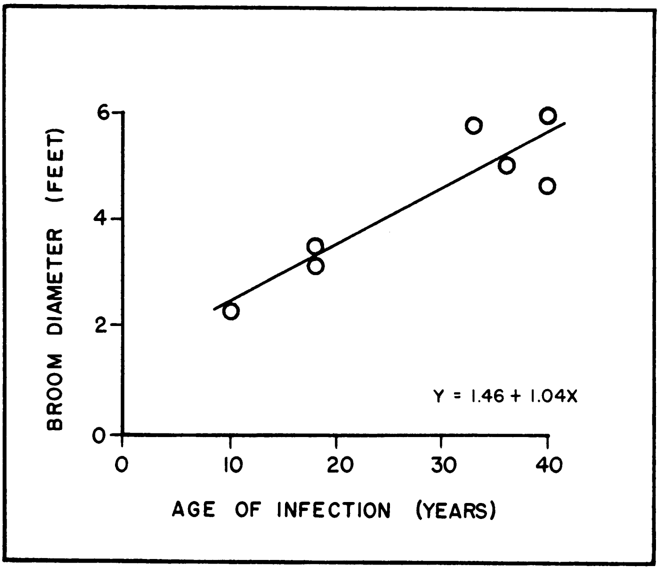

FIGURE 48.—Relationship between age of infection and diameter of typical brooms. Fort Valley Experimental Forest, Ariz.

Volunteer leader brooms are less common than typical brooms. A count made in two 70-year-old stands (table 10) showed that these averaged about 14 percent of the brooms present. However, the relative abundance of typical brooms and volunteer leader brooms is quite variable in different stands. Many of the infections in young trees grow into brooms of the volunteer leader type, but infections that occur later in the life of the trees usually develop into typical brooms. Thus, the proportion of volunteer leader brooms decreases as the stands become older, and that of typical brooms increases. Stands that are infected for the first time when the trees are past the sapling stage have few, if any, volunteer leader brooms.

Volunteer leader brooms, in general, occur lower on the bole and closer to the main stem than the other two types. As shown in table 11, for a count of 923 brooms in two 70-year-old pole stands,

TABLE 11.—*Relative abundance and height of the three types of brooms in two 70-year-old pole stands; combined data for areas A and B, Fort Valley Experimental Forest, Ariz.*

Height class (feet)	Type of broom					
	Typical		Volunteer leader		Weeping	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*
0–3	29	4	79	61		
3–6	174	22	42	32	4	44
6–10	276	35	7	5	5	56
10–15	188	24	1	1		
15–20	96	12	1	1		
20–30	20	3				
30–40	1					
Total	784	100	130	100	9	100

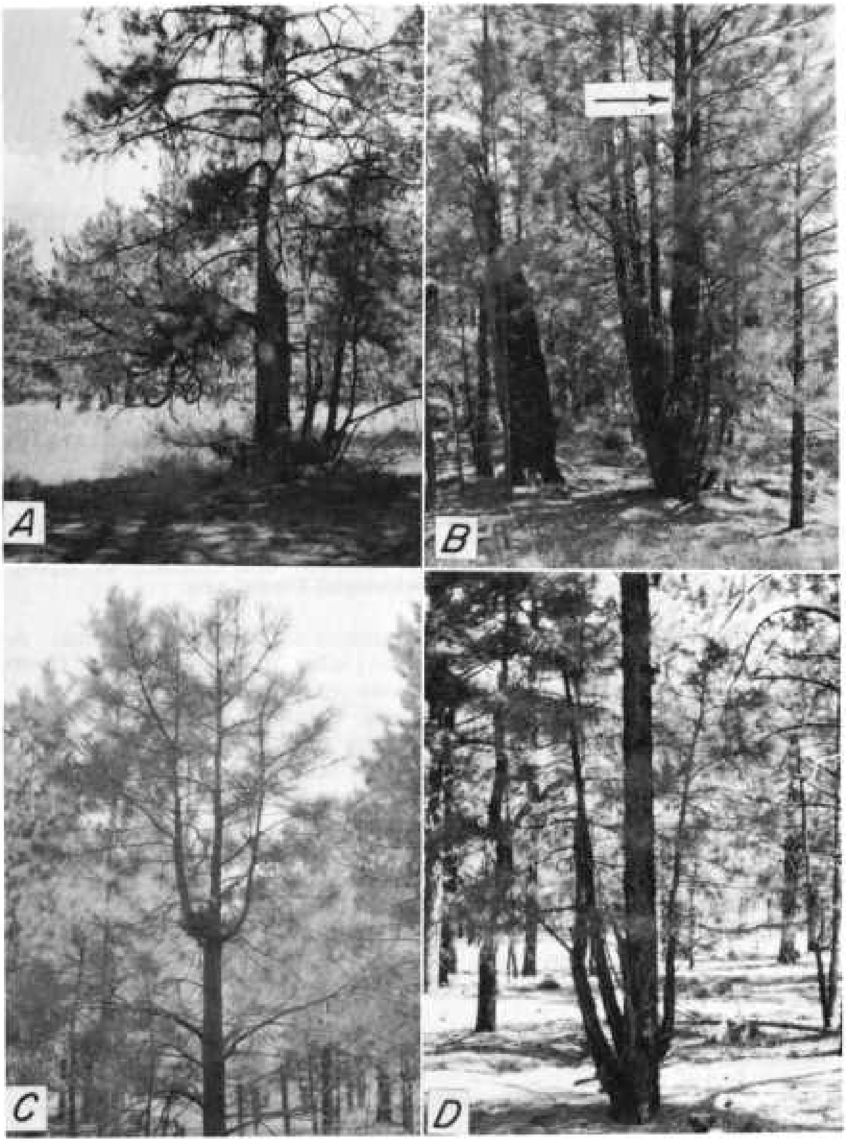

FIGURE 49.—Volunteer leader brooms in ponderosa pine. *A*, Tree with a volunteer leader broom (lower right) and a typical broom (center), showing how the former type usually occurs near the ground and close to the bole. *B*, Broom at the base of a 40-year-old tree. The branches on the broom have grown so rapidly that the original main stem (arrow) is scarcely distinguishable. *C*, Young bole infection (about 16 years old), showing how orientation of two branches near the infection has been so altered that they rival the original leader. *D*, Volunteer leader broom at the base of a pole-size tree. Fort Valley Experimental Forest, Ariz.

93 percent of the volunteer leader brooms occurred in the lower 6 feet of the bole and 61 percent in the lower 3 feet. Comparable figures for typical brooms were 26 percent and 4 percent, respectively. The average distance from the oldest part of the broom to the bole was 0.6 foot for volunteer leader brooms, 2.7 feet for typical brooms, and 1.7 feet for weeping brooms (table 12).

On one tree (fig. 49, *A*), an infection on a branch about one-half foot above the ground and about one-half foot from the bole developed into a volunteer leader broom, while on the same tree an infection 2 feet away from the main stem on a branch 4 feet above the ground developed into a typical broom.

Weeping Brooms

Weeping brooms, as the name implies, show a drooping habit of branching (fig. 50). This type of broom is much rarer than the other two types, and it amounted to only about 1 percent of the brooms in the two 70-year-old stands examined (table 10). Although the relationship between broom incidence and height above ground for weeping brooms is not as clearcut as it is for volunteer leader brooms (table 11), weeping brooms have not been seen higher than about 10 feet above ground.

Unlike infection in typical and volunteer leader brooms, infection in weeping brooms is systemic; that is, the endophytic system of the parasite keeps pace with the growth of the host parts and permeates every branch. In typical and volunteer leader brooms, the parasite is confined to a relatively localized area at the center or base of the broom (fig. 45).

Intermediate Broom Types

The three types of brooms just described are usually distinct, but intermediate brooms that have some features of two types are sometimes found. A typical broom with a vertical tendency of the main

TABLE 12.—*Bole-to-broom distance for the three types of brooms in a 70-year-old pole stand; area B, Fort Valley Experimental Forest, Ariz.*

Distance from bole to oldest part of broom (feet)	Type of broom					
	Typical		Volunteer Leader		Weeping	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*
0-1	22	10.0	49	91	2	33
1-2	59	27.0	5	9	2	33
2-3	58	27.0			1	17
3-4	42	19.0			1	17
4-5	19	9.0				
5-6	12	5.0				
6-7	5	2.0				
7-8	1	.5				
8-9	1	.5				
Total	219	100	54	100	6	100
	Feet		*Feet*		*Feet*	
Average distance	2.7		0.6		1.7	

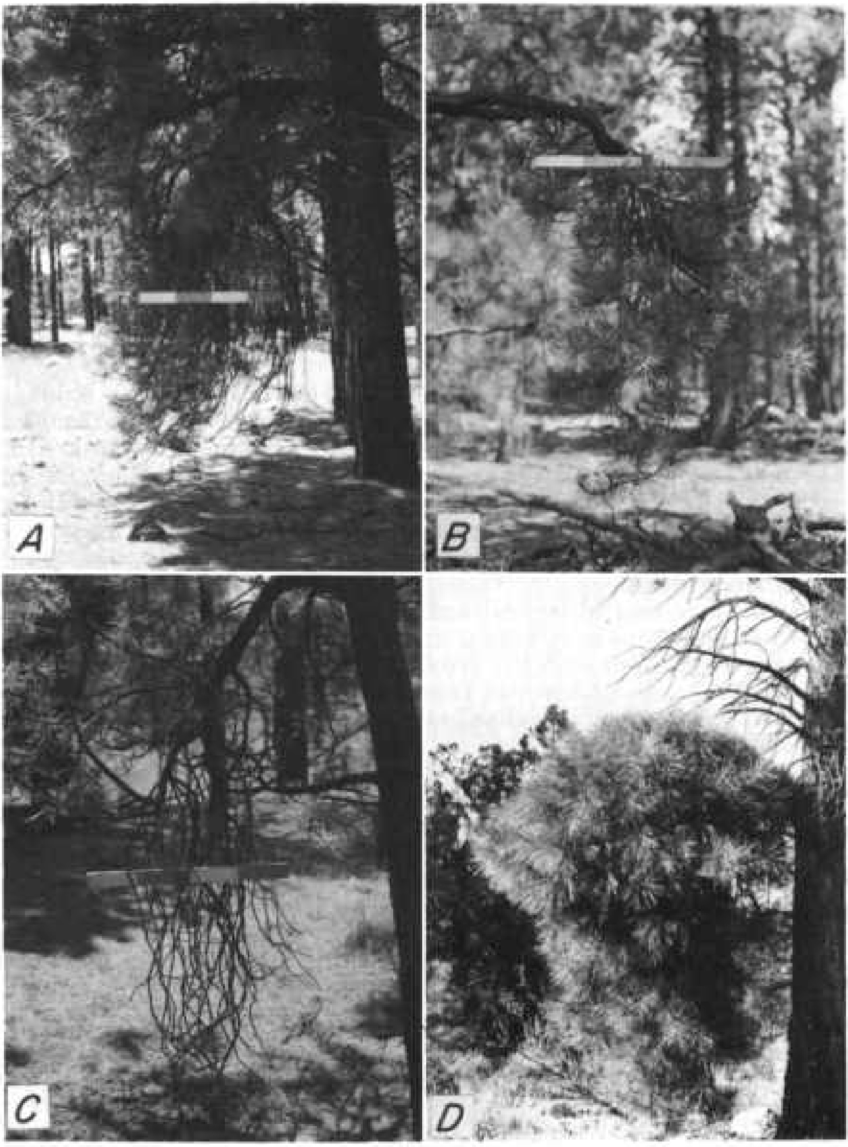

FIGURE 50.—Weeping brooms in ponderosa pine. *A*, Weeping broom on a large pole. *B*, Broom associated with a 30-year-old infection. *C*, Dead weeping broom, showing the long, slender branches. It was probably killed by shading. (*A*, *B*, and *C* brooms on the Fort Valley Experimental Forest, Ariz. Their size is indicated by a 2-foot rule.) *D*, An unusually dense weeping broom in the Grand Canyon National Park, Ariz.

branch is shown in figure 51, *A*, and a transition form between typical and weeping brooms is shown in figure 51, *B*. These intermediate types are rare.

DISCUSSION

The reason why three different types of brooms develop within a single host-parasite combination is not yet clear, but systemic dwarfmistletoe infections seem to be involved in the formation of at least one type.

Systemic Infections

A feature of dwarfmistletoe infection that has not been explained is the common occurrence of two types of shoot distribution on the same host species. These are (1) shoots clustered in a localized area of the branch, usually causing it to swell—a tufted type, and (2) shoots scattered along branches that show little or no swelling—a systemic type. Systemic *Arceuthobium* infections were recently discussed by Kuijt (1960). Gill (1935, p. 123) suggested that the type of infection was more a function of the individual host tree than anything inherent in the mistletoe. He noted that lodgepole pine infected with *Arceuthobium americanum* showed both types of infection with about equal frequency, but that the two seldom, if ever, occur on the same tree. However, for *A. vaginatum* f. *cryptopodum* on ponderosa pine, infections of the systemic type are found only on trees with the tufted type, for the former is an outgrowth of the latter.

Branchlets with systemic infections are invariably younger than the uninfected branchlets of the same branch (fig. 52). Thus, these infected branchlets arise from buds that have been dormant for some time and then stimulated into growth by the parasite. A characteristic of such infections is that all subsequent growth of the stimulated branchlet bears infection of the systemic type. Mistletoe shoots are commonly produced on internodes 2 years old and older, although sometimes they are seen on 1-year-old growth.

Counts made on the Fort Valley Experimental Forest showed that the proportion of two-needled fascicles was greater on branchlets bearing systemic infections than on uninfected branchlets of the same branch. Over 2,000 fascicles on 8 paired branchlets were examined. The ratio of two-needled to three-needled fascicles was 10:90 for uninfected branchlets and 28:72 for those bearing systemic infection. This is taken as further evidence that branches bearing systemic infections are not part of the normal branch system.

The nature of the ponderosa pine buds that develop into systemic infections is not yet known, but observations have shown that at least two types are stimulated by dwarfmistletoe. These are dormant whorl buds and needle fascicle buds. The dormant whorl buds (Cooperrider 1938) occur only at the nodes and are usually 3 to 5 millimeters high (fig. 53, *B*). These buds normally die and fall off after a few years, but if the terminal of the branch is removed or killed by grazing animals or tip moths, they are capable of developing into new branchlets. Small aborted needles ¼ to ¾ inch long are frequently found on the dormant whorl buds (fig. 53, *B*).

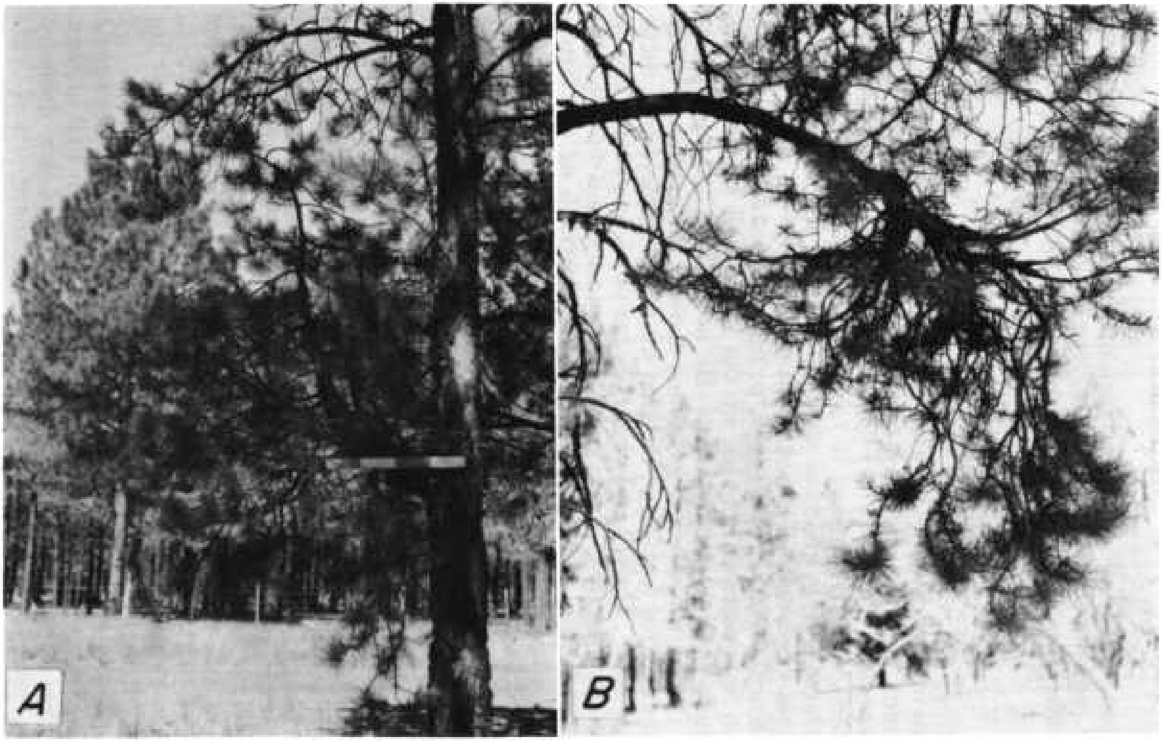

FIGURE 51.—Intermediate broom types in ponderosa pine: *A*, Typical broom with vertical tendency of the main stem, the Fort Valley Experimental Forest, Ariz. *B*, Broom in which the upper parts resemble that of a typical broom (markedly tapered branches, nonsystemic infection) while the lower parts exhibit characteristics of weeping brooms (drooping branches, systemic infection), the Grand Canyon National Park, Ariz.

FIGURE 52.—Systemic dwarfmistletoe infections on ponderosa pine: *A*, An infection (arrow) on the main stem of a branch on the twelfth internode and with two side branchlets bearing systemic infections. The upper branchlet has five internodes and the lower one seven, thus showing that they arose from buds that were inactive for 7 and 5 years, respectively. The 1957 terminal growth of these two side branchlets was about four times that of the main branch. Fort Valley Experimental Forest, Ariz. *B*, An older systemic infection; here only branchlets bearing systemic infections are living. The main branch (arrow) is dead beyond the point where the side branchlet arose. The infected branch is not swollen except at the point of junction with the main stem. Dwarfmistletoe shoots marked "s." Kaibab National Forest, Ariz.

In 1955, 43 dormant whorl buds adjacent to dwarfmistletoe infections were tagged and they are being observed periodically. By 1958, 12 of these buds (28 percent) had been stimulated by the parasite and had developed into branchlets. The remaining 31 pine buds (72 percent) and all dormant whorl buds not near dwarfmistletoe infections were either unchanged or dead after this period. The average height of the 12 stimulated buds during this 4-year period was as follows:

Year	*Average height (centimeters)*
1955	0.7
1956	1.7
1957	4.3
1958	8.2

One dormant bud 0.5 centimeter high in 1955 developed into a branchlet that was 20.7 centimeters high 3 years later. Figure 53, *C* shows a branchlet that is the outgrowth of a dormant whorl bud.

It is definitely known that both dormant whorl buds and needle fascicle buds (fig. 53, *A*) are stimulated by dwarfmistletoe, although stimulation of the latter is less frequent. However, since observations have not been made over periods long enough for dwarfmistletoe shoots to be produced on such stimulated growth, it is not certain whether growth from one or both bud types will develop into systemic infections. It seems most likely that systemic infections may be outgrowths of dormant whorl buds, because most branches with systemic infections originate at the nodes (fig. 52, *A*).

Possible Explanation for the Different Broom Types

Von Schrenk (1900) and Anderson and Kaufert (1959) suggest that host vigor is the primary factor determining the type of broom formed on spruce infected by *Arceuthobium pusillum*. For *A. vaginatum* f. *cryptopodum* on ponderosa pine, host vigor influences broom size, but it does not seem to be a factor in broom type.

Of the three types of brooms on ponderosa pine, two (typical brooms and volunteer leader brooms) are basically similar in that the parasite is confined to a localized area near the original point of infection. Weeping brooms differ in that the infection is of a systemic type. It is probable that weeping brooms are later stages of the systemic infections just discussed.

Dormant buds are probably involved in the formation of typical and volunteer leader brooms also, but just how the many branchlets arise in these brooms is not yet known. The difference between typical and volunteer leader brooms might best be explained on physiological grounds. It has been shown that when infection takes place near the main stem and close to the ground, a volunteer type broom usually develops; but, when infection occurs elsewhere, typical brooms are formed. It is apparent in both types that the apical dominance regime of the branch and tree is disrupted.

In typical brooms the terminal bud of the infected branch, which normally supplies auxin that limits growth of the secondary branches, is gradually weakened and killed. There is a definite brooming

FIGURE 53.—Stimulation of ponderosa pine buds by dwarfmistletoe. *A*, Needle fascicle buds: the shoots (s) of the parasite are just emerging from the bark, and the interfoliar bud (b) of an adjacent needle fascicle is starting to develop into a branchlet. From an artificial inoculation made in 1954 on a 1954 internode; photographed in 1957 (3 times natural size). Cibola National Forest, N. Mex. *B* and *C*, Dormant whorl buds: *B*, An undeveloped bud with aborted needles on a 9-year-old internode (X 0.4). *C*, A similar bud that developed into a branchlet (X 0.4). This branchlet was 3.8 centimeters high in 1957 when the photograph was taken and 0.3 centimeter high in 1955 when it was in a dormant condition similar to that in *B*. Fort Valley Experimental Forest, Ariz.

tendency of these branches even before the terminal is killed (fig. 47, *B* and *C*); the auxin-producing ability of the terminal bud is probably reduced for some time before it is finally killed.

In volunteer leader brooms, the terminal bud of the infected branch is not killed, but it no longer limits the development of the lateral branches; they grow directly upward as new leaders (fig. 49, *C*). Since the infection takes place near the main stem and close to the bole, it is possible that these leaders are supplied with high quantities of an auxin precursor, and that they are thus able to develop abundant auxin-supplying terminal buds.

Experiments involving dissection of terminals and application of auxins to infected and uninfected branches are needed to learn more of the auxin relations of broom formation.

SUMMARY

The dwarfmistletoe *Arceuthobium vaginatum* f. *cryptopodum* (Engelm.) Gill is the most important pathogen of ponderosa pine (*Pinus ponderosa* Laws.) in the Southwestern United States. The parasite is common in Arizona, New Mexico, Colorado, and Utah and it also occurs in a few localities in Nevada and Texas. About 36 percent of the commercial ponderosa pine acreage in Arizona and New Mexico is affected by this dwarfmistletoe. The disease causes mortality and growth reduction in infected trees, and it also lowers seed production and timber quality. Heavily infected trees are also more susceptible to attack by insects and other diseases.

A general description of the shoots, flowers, fruits, seeds, and endophytic system of the dwarfmistletoe is given along with a discussion of the pathological aspects of infection. The factors influencing the distribution of the parasite including stand type, stand history, and site factors are described.

Several biologic agents (fungi, insects, birds, and mammals) affect the parasite, but they do not appear to be important natural control agents. Presumably resistant trees have been found, but no tests of susceptibility have been carried out.

Chemical control of dwarfmistletoes is not yet feasible.

Pruning can be practiced to effectively reduce dwarfmistletoe if trees are only lightly infected and if infections do not occur in or near the trunk. Pruning guides developed from tests with infected branches are given.

Dwarfmistletoe can be reduced to an innocuous level by silvicultural control methods. The following procedures are recommended: (1) removal of all infected overstory trees, (2) removal or pruning of all infected trees in the understory, and (3) followup operations in all size classes. Control in lightly and moderately infected stands can be accomplished with relatively minor modifications of current cutting practices. The only additional work needed is the treatment of infected parts of the understory. Control in severely diseased stands necessitates heavier cuts and intensive followup operations.

Information is presented on the results of the following six studies on this dwarfmistletoe:

1. *Life history as determined by inoculations.* The seeds germinate within 1 month after they are expelled. Insects and other agents

destroyed many of the seeds, and only about 5 percent of the seeds planted resulted in infection. The more recent internodes are the most susceptible but some infection occurred on growth as old as 9 years. Over 90 percent of the infections first produced shoots during the third, fourth, and fifth years after the date of planting. Flowers were first produced in 5 years and the first mature fruits in 6 years from the date of planting. A 1:1 sex ratio exists for this species.

2. *Seed flight.* The average horizontal distance traveled by the seeds was 17.4 feet, with a maximum of 42.0 feet. There was a linear relationship between the logarithm of the number of seeds falling on a unit area and the distance from the seed source. The trajectories of seeds expelled at different angles were calculated. The natural angle of discharge averages 30° to 40° above the horizontal. The average initial velocity of the seeds is estimated at 45 feet per second.

3. *Seed dispersal period.* The dispersal period was measured during 3 successive years on the Fort Valley Experimental Forest, Ariz. The bulk of the seeds were expelled during the 3-week period including the last week in July and the first 2 weeks in August. There were only slight differences in the length of the seed dispersal period in the 3 years observed, but the number of seeds produced varied considerably from year to year.

4. *Rate of spread.* Measurements on spread of the parasite were made in 42 stands in Arizona and New Mexico. Infection in young stands progressed from an infected overstory at an average rate of 1.7 feet per year in stands where the crown canopy had not closed, and 1.2 feet annually in closed-canopied stands. The rate of lateral spread through even-aged stands averaged 0.9 foot per year.

5. *Effects on growth rate of the host.* Measurements of 1,600 trees of two age classes were made on the Mescalero-Apache Reservation, N. Mex., to determine the effects of various amounts of infection on the growth of ponderosa pine. There was a significant reduction in recent (last 5 years) radial increment only in trees in which at least two-thirds of the crown was infected. Recent radial increment in heavily infected trees was reduced 35 percent in 55-year-old stands and 52 percent in 140-year-old stands. There was a marked reduction in vigor of heavily infected trees of both age classes. The effect of dwarfmistletoe in heavily infected trees was most pronounced on recent radial increment and total volume, intermediate on height, and least on total diameter.

6. *Witches'-broom formation.* Three types of witches'-brooms associated with this parasite on ponderosa pine are described. The characteristics and relative abundance of the three types, and possible explanations of how they are formed, are discussed. Systemic dwarfmistletoe infections are shown to arise from dormant pine buds that are stimulated by the parasite.

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APPENDIX

KNOWN DISTRIBUTION

Known distribution of *Arceuthobium vaginatum* f. *vaginatum* in the United States, Mexico, and Guatemala. Basis for figure 1.

Country and State	Locality	Reference
United States:		
Arizona	Cochise and Pima Counties	Gill 1935.
New Mexico	Grant County	Do.
Mexico:		
Coahuila		Standley 1922.
Do	Sierra del Pino	Johnston 1944.
Chihuahua	Mesa Colorado	Gentry 1942.
D. F	Valle de Mexico	Roldan 1924.
Durango		Standley 1922.
Jalisco	Nevada de Colma	Tubeuf 1919.
Mexico [1]		Hemsley 1882.
Michoacan	Sierra de San Andres	Tubeuf 1919.
Do	Cerro Tancitaro, Rio Tepalcatepec	Leavenworth 1946.
Oaxaca [2]		Hemsley 1882.
Do		Standley 1922.
Do	Sierra de San Felipe	Tubeuf 1919.
Sonora	"Pine Ridge Pass"	Robinson and Fernald 1895.
Do		Standley 1922.
Tlaxcala	Montes de finca de San Diego Pinar.	Sosa 1939.
Vera Cruz [2]		Hemsley 1882.
Vera Cruz [1]	Orizaba	Do.
Vera Cruz [3]	Cofre de Perote	Gill 1935.
Guatemala	Alta Verapaz, Baja Verapaz, Zacapa, San Marcos, and Huehuetenango.	Standley and Steyermark 1946.

[1] As *Arceuthobium campylopodum.*
[2] As *Arceuthobium oxycedri.*
[3] The type locality of *Arceuthobium vaginatum.*

The distribution of *Arceuthobium vaginatum* f. *cryptopodum* on ponderosa pine by counties in the United States. The known distribution of the species based on collections and reports in the literature up to about 1934 was summarized by Gill (1935, pp. 179–181). New localities are indicated by parentheses. Basis for figure 1 (in part) and figure 2.

State and County	Reference or location
Arizona:	
Apache	Gill 1935.
Cochise	Do.
Coconino	Do.
Gila	Do.
Graham	Do.
Greenlee	(Apache National Forest, Alpine District, 1954).
Mohave	(Hulapai Mountain Park. Collected by Stuart R. Andrews, U.S. Forest Service, 1959.)
Navajo	Gill 1935.
Pima	Do.
Yavapai	Do.

State and County	Reference or location
Colorado:	
Archuleta	(3 miles west of Pagosa Springs, 1957.)
Boulder	Gill 1935.
Chaffee	Do.
Clear Creek	Do.
Conejos	Do.
Custer	Do.
Douglas	(8 miles east of Deckers, 1959.)
Elbert	(5 miles south of Elbert, 1959.)
El Paso	Gill 1935.
Fremont	Do.
Gilpin	Do.
Huerfano	Do.
Jefferson	Do.
La Plata	Do.
Larimer	Gill 1935. (Northern limit of the parasite. The species occurs within 15 miles of the Wyoming boundary, Redfeather Lakes area, 1957.)
Las Animus	Rogers 1953.
Mesa	(Manti-LaSal National Forest. Information from J. K. Stithem, U.S. Forest Service, April 22, 1960.)
Montezuma	(4 miles north of Dolores, 1957.)
Montrose	(Manti-LaSal National Forest. Information from J. K. Stithem, U.S. Forest Service, April 22, 1960.)
Park	Gill 1935.
Pueblo	(6 miles northwest of Rye, 1959.)
Rio Grande	Gill 1935.
Saguache	Do.
San Miguel	(6 miles east of Placerville, 1957.)
Teller	Gill 1935.
Nevada:	
Clark	(Clokey (1951) lists *Arceuthobium campylopodum* on ponderosa pine on Charleston Peak. However, an examination of one of Clokey's collections (No. 5432) at the Herbarium of Colorado State University revealed that this dwarfmistletoe is *A. vaginatum*. The plants are spring-flowering and the fruits mature in August. The change in nomenclature of this collection was confirmed by Dr. L. S. Gill. This Nevada location represents the western known limit of *A. vaginatum* f. *cryptopodum*.)
New Mexico:	
Bernalillo	Gill 1935.
Catron	Do.
Colfax	(Red River Pass, 1957.)
Dona Ana	Gill 1935.
Eddy	(Guadalupe Mountains, letter of March 23, 1960, from Dean M. Earl, U.S. Forest Service.)
Grant	Gill 1935.
Lincoln	Do.
Los Alamos	(West of Bandelier National Monument, 1955.)
McKinley	(Navajo Reservation, Chuska Unit, 1956.)
Otero	Gill 1935.
Rio Arriba	(Jicarilla-Apache Reservation, 1955.)
Sandoval	(Santa Fe National Forest, Jemez Division, 1955.)
San Juan	Gill 1935.
San Miguel	Do.
Santa Fe	Do.
Sierra	Do.
Socorro	(Cibola National Forest, San Mateo District, 1957.)
Taos	(La Junta, Carson National Forest, 1957.)
Torrance	(Red Canyon, Cibola National Forest, 1950.)
Union	Gill 1935.
Valencia	(Mt. Taylor, Cibola National Forest, 1957.)

State and County	Reference or location
Texas:	
Culberson	Gill 1935.
Jeff Davis	Do.
Utah:	
Emery	(Manti-LaSal National Forest. Information from J. C. Downing, U.S. Forest Service, April 22, 1960.)
Garfield	Gill 1935.
Grand	(Manti-LaSal National Forest. Information from J. K. Stithem, U.S. Forest Service, April 22, 1960.)
Kane	(Dixie National Forest. Letter of July 6, 1959, from H. L. Ketchie, U.S. Forest Service.)
San Juan	Gill 1935.
Sevier	(Fishlake National Forest. Letter of August 11, 1959, from William A. Worf, U.S. Forest Service.)
Wayne	(Letter of October 28, 1957, from Dr. James L. Mielke, Intermountain Forest and Range Experiment Station, Logan, Utah.)

SUMMER WEATHER, 1955–57

Summary of weather on the Fort Valley Experimental Forest during the summers of 1955, 1956, and 1957. The height of the seed dispersal period of drawfmistletoe is from July 15 to August 15, while that for germination is August 15 to September 15.

Period	Mean temperature		Average precipitation per day	Days with measurable precipitation	Time per day when relative humidity was approximately 100 percent
	Maximum	Minimum			
	° F.	*° F.*	*Inches*	*Percent*	*Hours*
July 1–15	81	40	0.02	13	(1)
July 16–31	77	46	.16	67	11.2
Aug. 1–15	78	45	.15	49	10.5
Aug. 16–31	76	42	.09	33	8.4
Sept. 1–15 [2]	82	38	0	0	3.9
Sept. 16–30 [2]	76	31	0	0	2.8

[1] Not recorded.
[2] Data for 1955 and 1956.

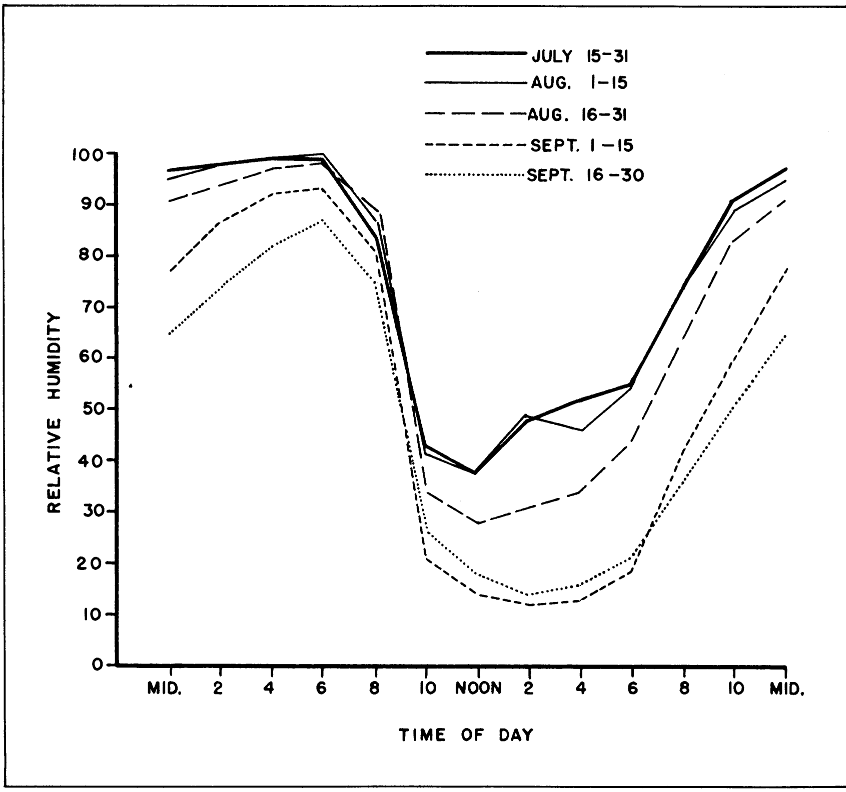

FIGURE 54.—Daily relative humidity by 2-week periods during the time of dwarfmistletoe seed dispersal and germination. Data for 1955, 1956, and 1957. Fort Valley Experimental Forest, Ariz.

Ballistic Computations of Dwarfmistletoe Seed Flight

Relationship Between Initial Velocity and Vertical Height of Seed Flight (Fig. 27)

$$H=\frac{m^2}{c^2}g\ ln\left(\frac{g+\frac{c}{m}V_o}{g}\right)-\frac{m}{c}V_o$$

Where H = maximum vertical height of seed flight (centimeters)

m = mass of seeds (0.0024 grams) (specific gravity estimated as approximately 1.0)

$c=\frac{\text{frictional force}}{\text{terminal velocity}}=\frac{mg}{V_t}$

V_t = terminal velocity = 750 centimeters per second

g = acceleration due to gravity = 980 centimeters per second^2

ln = natural logarithm of

V_o = initial velocity in centimeters per second

Time of seed flight

The time of seed flight for a seed shot directly upward can be calculated from this formula:

$$t=\frac{V}{g}$$

Where t = time in seconds
V = initial velocity (45 feet per second)
g = acceleration due to gravity (32 feet per second^2)

$t={}^{45}\!/_{32}=1.4$ seconds

This is the time required for the seed to reach the highest point; the time for the complete flight back to the level of the point of discharge is twice this or about 2.8 seconds.

Time taken for seed to leave the fruit

If a body starts from rest and travels for t seconds, its average velocity is $\frac{1}{2}V$ during the time it travels over a distance d.

$$d=\tfrac{1}{2}\mathrm{V}\cdot t,\quad t=\frac{2d}{V}$$

In this case, d=0.3 centimeter or the distance traveled by the seed while leaving the fruit.

V_o=45 feet per second =1370 centimeters per second
then,

$$t=\frac{(2)\,(0.3)}{1370}=0.00044 \text{ second}$$

$$\text{or approximately } \frac{1}{2300} \text{ second}$$

Distance to reach terminal velocity

The distance in free fall (starting at zero velocity) to reach terminal velocity can be approximated by this formula:

$$d=\frac{V^2{}_t}{2g}$$

where V_t = terminal velocity = 24.5 feet per second
g = acceleration due to gravity = 32 feet per second^2

$$d=\frac{(24.5)^2}{(2)\,(32)}=9.4 \text{ feet, or approximately 10 feet}$$

Kinetic energy of the seed as it leaves the fruit

$$\text{Kinetic energy}=\tfrac{1}{2}\,m\,V^2$$

where m = mass of seeds = 2.4 milligrams
V_o = initial velocity = 1370 centimeters per second

$$\text{Kinetic energy}=\frac{(0.0024)\,(1370)^2}{2}=2.3\times10^3 \text{ ergs.}$$

Acceleration of dwarfmistletoe seeds

The propelling force acts on about two-thirds of the seeds which average about 3 millimeters in length; thus the maximum speed is attained when the seed has traveled about 2 millimeters. The time taken for the seed to travel this distance is

$$t=\frac{2d}{V_o}$$

where $d=0.2$ centimeter

$V_o=1370$ centimeters per second

$$\text{then, } \frac{(2)\,(0.2)}{1370}=\frac{1}{3400} \text{ second}$$

The acceleration of the seeds is thus (3400) (1370) or 4.7×10^6 centimeters per second^2. As the acceleration due to gravity is 980 centimeters per second^2, the acceleration of the dwarfmistletoe seeds is nearly 5,000 times gravity.

SEED FOUND ON TRAPS, 1955–57

Number of seeds found on each of the 30 seed traps in 1955, 1956, and 1957. Fort Valley Experimental Forest, Ariz.

Type of stand and trap number	1955	1956	1957	Total	Type of stand and trap number	1955	1956	1957	Total
Pole:					Mature:				
1	9	73	37	119	18	5	25	11	41
2	6	82	38	126	19	4	33	7	44
3	[1] 51	139	[1] 117	307	20	1	5	1	7
4	27	[1] 154	[1] 67	248	21	14	7	10	31
5	18	109	[1] 70	197	22	11	14	18	43
6	2	44	20	66	23	17	11	8	36
7	20	[1] 248	51	319	24	17	33	17	67
8	9	[1] 157	32	198	25	13	12	8	33
9	7	142	33	182	26	14	15	8	37
10	18	95	39	152	27	8	13	13	34
11	[1] 38	[1] 198	[1] 103	339	28	5	8	3	16
12	10	109	26	145	29	9	12	8	29
13	16	78	11	105	30	17	19	15	51
14	[1] 35	136	33	204					
15	20	149	50	219	Total	457	2, 251	926	3, 634
16	20	78	28	126					
17	16	53	44	113	Average seeds per trap	15	75	31	40
					Average seeds per square foot	1. 5	7. 5	3. 1	4

[1] Number of seeds more than twice the average for the year.

RATE OF SPREAD OF INFECTION

Summary of the 33 plots established to measure the rate of spread of dwarfmistletoe from overstory stands to adjacent young stands. The distances are a result of infection directly from the overstory plus lateral spread in the young stand. Arranged in order of increasing stand age in each density class.

Type of stand, plot number, and location	Average age of stand	Average maximum distance of infection		Annual rate of spread
	Years	*Feet*	*Basis* [1]	*Feet*
Open young stands:				
20. Mescalero Reservation, N. Mex	23	61	1	2.7
25. Fort Valley Experimental Forest, Ariz	26	55	1	2.1
26. ----do	27	37	1	1.4
29. ----do	27	47	1	1.7
15. ----do	30	39	2	1.3
16. Kaibab National Forest, Ariz	30	39	1	1.3
32. Fort Valley Experimental Forest, Ariz	31	39	1	1.3
7. Mescalero Reservation, N. Mex	32	65	13	2.0
8. ----do	32	68	6	2.1
19. Fort Valley Experimental Forest, Ariz	33	59	1	1.8
18. Kaibab National Forest, Ariz	33	72	2	2.2
9. Mescalero Reservation, N. Mex	34	57	3	1.7
12. ----do	35	60	5	1.7
24. Fort Valley Experimental Forest, Ariz	37	50	1	1.4
34. ----do	37	60	1	1.6
11. Mescalero Reservation, N. Mex	40	90	1	2.2
22. Fort Valley Experimental Forest, Ariz	41	53	1	1.3
23. ----do	41	54	1	1.3
21. ----do	41	68	1	1.7
42. ----do	43	88	1	2.0
39. ----do	49	77	1	1.6
Average or total of 21 plots	34	59	46	1.7±0.1
Dense young stands:				
14. Fort Valley Experimental Forest, Ariz	30	31	2	1.0
13. ----do	30	46	2	1.5
33. ----do	31	39	1	1.3
10. Mescalero Reservation, N. Mex	34	53	1	1.6
28. Fort Valley Experimental Forest, Ariz	37	45	1	1.2
27. ----do	37	51	1	1.4
35. ----do	48	50	1	1.0
36. ----do	48	68	1	1.4
37. ----do	49	61	1	1.2
38. ----do	49	55	1	1.1
40. ----do	49	55	1	1.1
41. ----do	51	56	1	1.1
Average or total of 12 plots	41	51	14	1.2±0.1

[1] Number of directions measured.

Summary of the 6 plots established to measure the rate of lateral spread of dwarfmistletoe through even-aged ponderosa pine stands.

Plot number and location	Measurements on each plot	Approximate stand age	Length of time since infection	Average maximum distance of infection	Annual rate of spread
	Number	*Years*	*Years*	*Feet*	*Feet*
2. Grand Canyon National Park, Ariz	1	50	33	28	0.9
12. Mescalero Reservation, N. Mex	5	150	35	41	1.2
17. Kaibab National Forest, Ariz	1	50	39	35	.9
31. Fort Valley Experimental Forest, Ariz	1	70	48	40	.8
30. Do	1	70	48	42	.9
1. Grand Canyon National Park, Ariz	2	100	59	57	1.0
Average or total of 6 plots	11	----------	44	40	0.9±0.06

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